Face Adaptation:

Behavioural and electrophysiological studies on the perception of eye gaze and gender

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1. Preface

The effortless recognition of other people is a fundamental basis of human social life. Among the several sources of information which possibly enable us to identify a person, the human face is certainly the most reliable and prominent one. Mostly we are very fast and efficient in distinguishing many different familiar individuals from their faces and are not even aware of how impressive this ability is. Moreover, apart from information about person identity, human faces provide us with a broad range of other socially relevant information, even if a person is unfamiliar to us: looking at the face of a person enables us to categorise it according to its gender, age, and ethnic background. The analysis of facial movements, especially lip movements, improves our speech comprehension and the correct interpretation of the emotional state of another person allows us to behave adequately in social situations.

A wealth of information important for social interactions can be derived from solely analysing the eye region of a face, which provides us with information about the emotional, attentional, and cognitive state of a person and also plays an important role in exercising social control, e.g. in communication situations.

Despite the long tradition of face perception research, the mechanisms and brain structures underlying the perception of social signals in faces have not yet been completely resolved. In the last ten years an experimental approach which had traditionally been applied to the analysis of low-level vision has turned out to be also very fruitful for investigating how specific aspects of faces are being processed and represented. The analysis of perceptual adaptation to these aspects in faces (e.g. gender or gaze direction) allows insight into the nature and selectivity of their respective neural coding and reveals relevant information about how faces are mentally represented. Perceptual adaptation paradigms can therefore provide a useful tool in finding out how the complex analysis of face stimuli works. In a series of four studies, the present work aims at a further investigation of eye gaze and gender adaptation processes. Combining adaptation paradigms with the high time resolution of electrophysiological recordings in event-related potential studies, a deeper insight into both the neural correlates of selective adaptation processes and the timing parameters of the processing of eye gaze and gender information is the major goal of this thesis.

I am deeply grateful to the people who supported me while I worked on this dissertation. First and foremost, I would like to express my gratitude to Stefan Schweinberger for being such an enthusiastic supervisor, for giving me the impression that his door is always open for me, and for encouraging me to pursue a career in research. He not only allowed me to greatly profit from his experiences and advice but also provided me with opportunities to go to conferences and present my work to other scientists. During the last three years I always felt able to work independently yet never left alone. Also, he is responsible for the friendly and supportive atmosphere in our team which I enjoy being a part of.

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2. Introduction

2.1 Face Perception

Humans have an outstanding ability to learn and memorise faces. Irrespective of how many people we already know we are always able to also learn the faces of those people we newly meet. The duration of the memory for faces seems to be infinite: even after time intervals as long as thirty years faces can still be recognised very accurately (for a review, see Bahrick, Bahrick, & Wittlinger, 1975). At the same time, the nature of our face representations seems to be very flexible and allows us to recognise people even though the appearance of their faces might have changed due to makeup, aging, or changes in weight. We are far from fully understanding all of the mechanisms and neural structures involved in the encoding, memorising and recognition of faces although many studies have been examining these topics and have accumulated much information about the way faces are perceived. The following section is designed to give a short review of important findings and open questions among face researchers. First, there will be a short overview of the fundamental questions and empirical findings that have been discussed with regard to face perception research (2.1.1) followed by a more detailed summary on specific findings related to the perception of eye gaze (2.1.2) and gender (2.1.3) which are of special relevance for the studies reported in this work.

2.1.1 General principles and models on face perception

Specificity

The determination of the degree to which the processes underlying face perception are specific for that object category is certainly one of the most prominent aims in current research. There are different views on this aspect, with one position assuming that the perception of faces is ‘special’ in a way that our perceptual system treats them differently from all other visual objects with special brain structures solely processing faces (Kanwisher, 2000). An alternative position, however, claims that faces are highly relevant visual objects for which we have gained large expertise and suggests that any possible visual category of similarly high expertise should elicit the same ‘special’ processing mechanisms and involve the same brain structures (Tarr & Gauthier, 2000). A consensus has not yet been found in this debate and there seems to be evidence for either view. Developmental studies, for example, showing that newborn babies track moving faces farther than other objects (Johnson, Dziurawiec, Ellis, & Morton, 1991) suggest that humans have a strong predisposition to process faces in a privileged way compared to other visual objects. Additional support for the assumption that faces are ‘special’ comes from studies on the so-called face-inversion effect (Yin, 1969) which describes that inverted faces are more difficult to recognise than inverted objects (for a review, see Valentine, 1988). Similarly, it has been shown that the inversion of the eye and mouth regions in a face leads to a very grotesque facial appearance, but this can hardly be detected when the whole face is inverted (Thompson, 1980). These findings suggest that the recognition of faces and objects are not functionally identical and that the accurate perception of faces is somewhat bound to their presentation in a normal, i.e. upright, orientation. Electrophysiological studies provided further evidence for differences in face and object processing. Single unit recordings in monkeys revealed the existence of cells in the inferior temporal cortex which respond strongly to monkey faces but show little response to the presentation of other visual objects (Baylis, Rolls, & Leonard, 1987). This idea of distinct neuroanatomical structures underlying the processing of faces and objects is also supported by neuropsychological research. The existence of patients selectively suffering from *prosopagnosia* (i.e. a severe impairment in face recognition) and others selectively suffering from *object agnosia* (i.e. a severe impairment in object recognition) with unimpaired face recognition suggests a double dissociation between face and object processing, with differences in the functional mechanisms and anatomical structures underlying them (DeRenzi & diPellegrino, 1998; Evans, Heggs, Antoun, & Hodges, 1995; Moscovitch, Winocur, & Behrmann, 1997).

There is also empirical evidence against the assumption of face-specificity. Non-face objects of large visual expertise have been shown to elicit processing strategies similar to that of human faces (Diamond & Carey, 1986; Gauthier & Tarr, 1997) and to recruit brain structures which were originally believed to be solely dedicated to face processing (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). These findings will be described in greater detail in the following sections.

Features and configurations

Two different kinds of information have generally been assumed to play an important role in face perception. Featural information refers to the information contained in the isolated facial parts such as eye colour, shape of the lips, or form of the eyebrows. Studies exploring the relative importance of different facial features suggest that the eyes or eyebrows are the most important features for face recognition, followed by the mouth and the nose (Fraser, Craig, & Parker, 1990; Haig, 1986; Sadr, Jarudi, & Sinha, 2003). The second kind of information in faces, namely configural information, refers to the spatial relationships of the facial parts. Maurer, LeGrand and Mondloch (2002) distinguish between three types of configural information: first-order spatial relations that define a stimulus as a face (i.e. two eyes positioned above a nose which is located above the mouth), holistic information which leads to the perception of the overall *gestalt* of a face, and second-order relations which are represented in the spatial relationships between the facial features and which are believed to be of great importance for individual face recognition (see Diamond & Carey, 1986, for a first dissociation of first-order and second-order spatial information). Although the exclusive analysis of facial features allows for a correct identification of facial stimuli (Schwaninger, Lobmaier, & Collishaw, 2002) configural information has long been discussed to be the key element of face processing in its most naturalistic, i.e. upright, orientation (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002; Tanaka & Farah, 1993; but see Hole, George, Eaves, & Rasek, 2002). When inverting the image of a face, however, the analysis of spatial information is thought to be hampered (Collishaw & Hole, 2002; Freire, Lee, & Symons, 2000; Thompson, 1980) leading to the face inversion effect (Yin, 1969; for a review, see Valentine, 1988). In the case of this unnatural orienting the processing of faces is believed to mainly rely on the analysis of feature information (Diamond & Carey, 1986; Farah, Tanaka, & Drain, 1995; Thompson, 1980). The fact that such a pronounced preference of configural analysis in upright stimuli could not be observed in the perception of other visual objects (Tanaka & Farah, 1993) and seemed to be applied mandatorily even under conditions in which a feature-based processing would have been more appropriate (Farah, Wilson, Drain, & Tanaka, 1995) led to the conclusion that the degree of dependence on configural information might be face-specific. This interpretation, however, was strongly challenged by the findings of Diamond and Carey (1986) who also found inversion effects for dog faces in a study testing dog experts. A further study underlining the relevance of visual expertise was conducted by Gauthier and Tarr (1997) who trained participants to discriminate between ‘greebles’, a homogeneous class of artificial, complex three-dimensional objects, which was designed in order to create a category of stimuli whose characteristics are comparable to those of faces (i.e. they consist of featural and configural information and have a high degree of overall similarity) whereas novices do not perceive them as faces. After extensive training, greeble experts showed the same preference for configural analysis that had formerly been considered to be unique to face perception. In line with this, a recent study showed that greeble experts presented with inverted greeble stimuli show an inversion effect of similar magnitude as the one for human faces (Ashworth, Vuong, Rossion, & Tarr, 2008). These findings provided strong evidence for the assumption that the special processing strategies applied to faces reflect expertise-specific perception of a homogeneous object class rather than purely face-specific processes (but see Duchaine, Dingle, Butterworth, & Nakayama, 2004, for a case study reporting normal greeble learning in a participant suffering from developmental prosopagnosia, a finding which severely challenged the idea that face and greeble perception are based on the same mechanisms and brain structures).

Electrophysiological and imaging studies on face processing

Event-related potential (ERP) studies have reported remarkable differences in the electrophysiological brain potentials following face and object presentation. The first results indicating the existence of an electrophysiological potential with a high preference for face stimuli compared to other objects were published by Jeffreys (Jeffreys, 1989; Jeffreys & Tukmachi, 1992). These studies reported a positive potential at electrode Cz at a peak latency of 150-200 ms to preferentially respond to faces as compared to other visual stimuli. Jeffreys (1989) named this component the ‘vertex positive potential’ (VPP) and stressed that the scalp distribution observed in his studies was well consistent with bilateral sources located in the temporal cortex. The VPP was found to be highly sensitive towards face orientation with face inversion leading to a reduction in amplitude and an increase in latency (Jeffreys, 1989; for a review, see Jeffreys, 1996).

Later, using a different and larger set of electrodes and a nose reference, Bentin et al. (Bentin, Allison, Puce, Perez, & McCarthy, 1996) described the N170, a negative deflection over occipitotemporal electrodes which is usually more pronounced over the right than left hemisphere. The N170 component has been assumed to reflect the same brain processes and underlying sources as the VPP (Joyce & Rossion, 2005) and has been found to be larger in response to whole faces or face parts as compared to other objects (Carmel & Bentin, 2002; Eimer, 1998; McCarthy, Puce, Belger, & Allison, 1999). However, the idea of a purely face-specific nature of the N170 (Bentin et al., 1996) was strongly challenged by findings that the N170 also responds to other visual objects such as car fronts (Schweinberger, Huddy, & Burton, 2004), animal faces (Rousselet, Mace, & Fabre-Thorpe, 2004), non-face objects such as greebles (Rossion et al., 2002), and other objects of expertise (Tanaka & Curran, 2001). In sum, these studies therefore suggest the N170 component to be characterised by a large degree of face-sensitivity rather than face-specificity.

Interestingly, the N170 has been shown to be largely affected by stimulus inversion, with reports of enhanced amplitudes and/or latencies in response to inverted as compared to upright faces (Carbon, Schweinberger, Kaufmann, & Leder, 2005; Itier & Taylor, 2002; Linkenkaer-Hansen et al., 1998; Rossion et al., 2000) and similar inversion effects in response to objects that had been trained to an expertise level (Ashworth et al., 2008; Rossion et al., 2002). This large effect of orientation on the N170 suggests that the loss of configural information due to inversion slows down early face processing (Rossion et al., 2000). Together with studies showing that the N170 is unaffected by the familiarity of faces (Bentin & Deouell, 2000; Rossion et al., 1999; Schweinberger, Pickering, Burton, & Kaufmann, 2002) these results indicate that the N170 reflects an early stage of face processing, i.e. the structural encoding of faces, and does not reflect the recognition process itself.

A later ERP component with sensitivity to human faces, however, has been shown to be influenced by face identity and is believed to represent the stage of individual face recognition. The N250r is evoked by repetition priming, i.e. it can be observed following face repetition but is absent in trials providing no face repetition (Schweinberger et al., 2004) and has been shown to be larger for familiar than for unfamiliar faces (Pfütze, Sommer, & Schweinberger, 2002; Schweinberger, Pfütze, & Sommer, 1995). A study reporting increasing N250r amplitudes from unknown over famous to personally familiar faces suggested that the component reflects the activation of stored structural face representations underlying the recognition of individual faces (Herzmann, Schweinberger, Sommer, & Jentzsch, 2004). The N250r typically arises over inferior temporal areas especially of the right hemisphere and its source has been located in the right fusiform gyrus (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002; Schweinberger et al., 2004).

This is in line with earlier neuroimaging studies comparing the brain activity when participants were either viewing pictures of objects or faces. These studies suggested the fusiform gyrus to be selectively involved in the perception of faces (Kanwisher, Chun, McDermott, & Ledden, 1996) which led to naming this structure the “Fusiform Face Area” (FFA, Kanwisher, McDermott, & Chun, 1997). It has to be considered, however, that other studies suggested that the FFA is not specific to the perception of faces per se but is part of a widely distributed system involved in the perception of both faces and other objects (Haxby, Hoffman, & Gobbini, 2000; Haxby, Hoffman, & Gobbini, 2002). FFA activation in response to non-face visual objects of expertise has been shown to be similar to that evoked by human faces (Tarr & Gauthier, 2000). A very recent line of research using imaging methods with improved spatial resolution such as functional magnetic resonance imaging-adaptation, pattern analysis, and high-resolution functional magnetic resonance imaging (HR-fMRI, for a review, see Grill-Spector & Sayres, 2008) offers an explanation for these seemingly contradictory results. Recent evidence from a HR-fMRI study suggests a fine scale organisation of the fusiform face area containing a heterogeneous structure, with some neural populations being highly selective to human faces and others being highly selective to non-face objects (i.e. faces, animals, cars, and sculptures, Grill-Spector, Sayres, & Ress, 2006b). Importantly, the data of Grill-Spector et al. (2006b) implied larger numbers of face-specific than non-face object-specific cell populations in the FFA and are therefore able to explain the larger overall activity in response to faces as compared to objects which were reported in most standard-resolution fMRI (SR-fMRI) studies (Avidan, Hasson, Hendler, Zohary, & Malach, 2002; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Peelen & Downing, 2005). The authors therefore concluded “that the maximal FFA responses to faces and the intermediate responses to nonfaces measured with SR-fMRI reflect averaging across heterogeneous and highly selective populations of different sizes, rather than higher selectivity to faces” (Grill-Spector et al., 2006b, p. 1182).

Models on face perception

Irrespective of their degree of face-specificity, it is important to understand which mechanisms form the basis of our ability to recognise faces. The most influential models concerning the mechanisms underlying face perception are probably those proposed by Bruce and Young (1986) and Haxby, Hoffman, and Gobbini (2000). The cognitive model of face recognition by Bruce and Young (1986) assumes a series of processing stages to be necessary for the recognition of familiar faces (see Figure 1 for a schematic illustration of the model). First, faces are claimed to be *structurally encoded*, which includes two processes: the view-centred pictorial analysis of a face allows for the analysis of the current visual composition and provides input for the stages of expression analysis and facial speech analysis. Further, a structural encoding of the face composition irrespective of viewpoint, lighting conditions, or the current expression allows for a processing of the relatively stable aspects of faces. At the next stage, the results of this structural encoding process are thought to be compared to stored representations of faces, so-called *face recognition units* (FRU). If the information from the structural encoding stage matches the information of an FRU, it is assumed that the corresponding *person identity node* (PIN) will be activated and person-related semantic memory can be accessed. PINs are also thought to be accessible by sensory input of other modalities, e.g. voices or written names. As a final stage of person recognition the process of "*name generation*" allows for accessing the person's name.

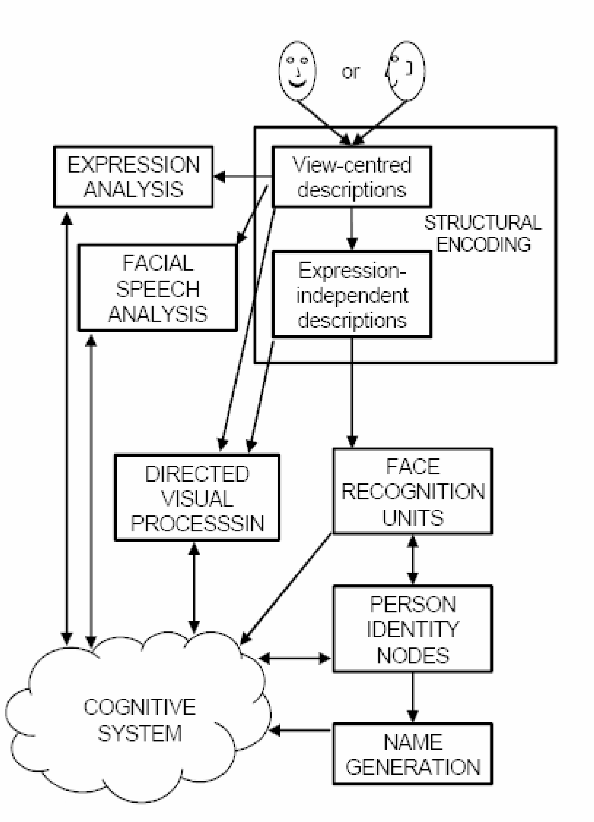


Figure 1: Schematic illustration of the cognitive model of face perception by Bruce and Young (1986).

The neurocognitive model of face perception by Haxby et al. (2000) proposes a distinction between the processing of changeable and invariant aspects of faces. It assumes that the processing of relatively changeable aspects in faces (e.g. eye gaze, emotional expression, and lip movements) serves as a basis for perceiving the kind of information which is of special relevance for social interactions (i.e. eye gaze direction and emotional state) whereas the analysis of invariant aspects of faces is believed to underlie the recognition of individual faces. Haxby et al (2000) suggest that the analysis of faces is performed by a core and an extended system (see Figure 2). The core system is assumed to serve the visual analysis of faces, with invariant aspects underlying recognition and being processed in the fusiform gyrus and changeable aspects being analysed in the superior temporal sulcus (STS). The extended system is thought to be represented by neural systems for other cognitive functions (e.g the auditory cortex or the limbic system) which support the structures of the core system in order to extract meaning from faces.

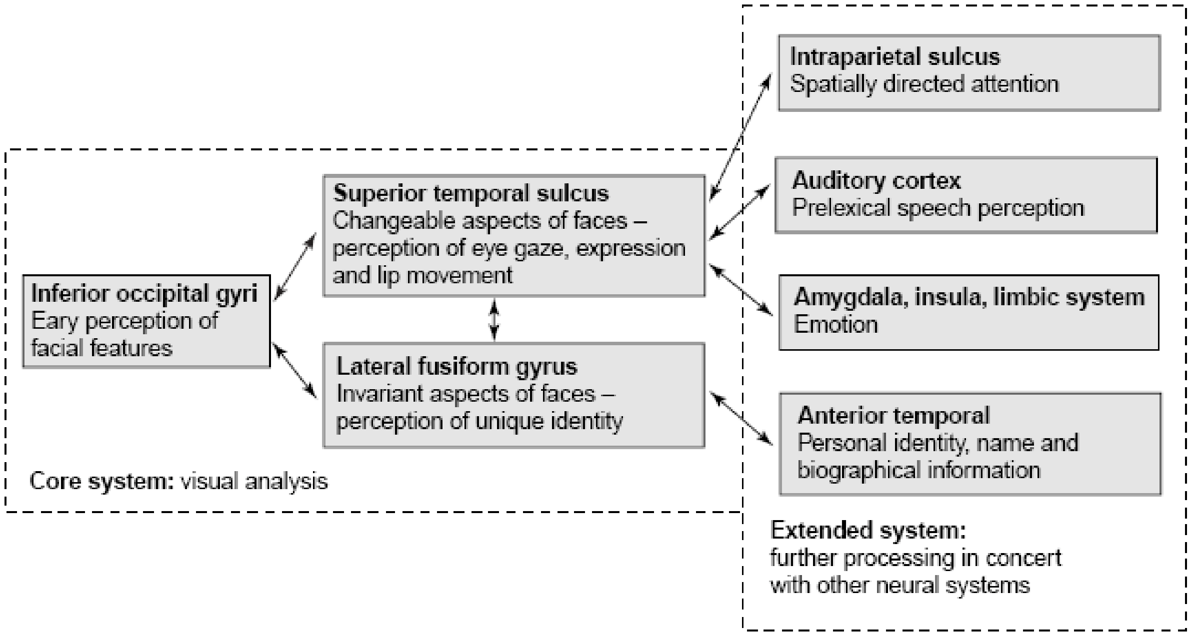


Figure 2: Schematic overview of the neurocognitive model of face perception by Haxby et al. (2002) illustrating the neural structures assumed to be part of the core and the extended system. Figure taken from Haxby et al. (2002).

To summarise, both the Bruce and Young model and the Haxby model underline the importance of processing and integrating both relatively stable aspects mediating the recognition of familiar faces and relatively changeable aspects mediating the perception of important social signals such as the eye gaze direction or the emotional state of both familiar and unknown faces.

2.1.2 Gaze Perception

Among the single visual features in human faces, the eyes are probably the most prominent and important ones. The efficient perception of another person’s eye region can help us to derive information about the attentive, emotional, and cognitive state of that person and allows us to modify our actions accordingly. Findings of deficits in the processing of gaze direction in autistic people (Dichter & Belger, 2007; Wallace, Coleman, Pascalis, & Bailey, 2006) have been suggested to underline the high correlation of the abilities to perceive information from eye gaze and to act appropriately in social situations. Humans have been shown to be highly sensitive to other people’s gaze directions, being able to reliably perceive even gaze deviations as small as only 1.4° (Cline, 1967).

Most importantly, the directional content in the eye gaze of others serves as an important basis for detecting their focus of spatial attention. Moreover, perceiving the direction of gaze in others has been suggested to trigger fast ‘reflexive’ attentional shifts in the observer (Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999; Langton & Bruce, 1999). That is, in cueing experiments participants are typically faster to detect a target at a location that corresponds to the gaze direction of a previously presented face than to respond to a target that appears at an uncued location (Langton & Bruce, 1999). This indicates that participants, even though correctly informed that gaze direction is uninformative with regard to the target location, can obviously not prevent shifting their attention to a gazed-at location. It is probably worth considering that both the ability to correctly estimate where another person is looking and the tendency to direct one’s own attention to the same location might have been important abilities in the evolution of mankind. Considering this evolutionary perspective it has been speculated that the general attentional effect should be modulated by the emotional expression of the observed face. One would intuitively expect that someone looking in a certain direction with a fearful expression most probably indicates the presence of something threatening at that location and should therefore induce a larger gaze cueing effect than a face displaying a neutral emotional expression. Surprisingly, the results of emotional gaze cueing studies were very inconsistent, with some finding no effect of emotional expression on the magnitude of gaze cueing effects (Hietanen & Leppanen, 2003) and others, using more naturalistic stimuli, finding fearful faces to induce stronger gaze cueing than happy faces in normal participants (Putman, Hermans, & Van Honk, 2006; Tipples, 2006) or only in participants with high levels of trait anxiety (Mathews, Fox, Yiend, & Calder, 2003).

Several studies have shown that the information contained in eye gaze interacts with other aspects of face perception and recognition. Compared to normal subjects, some prosopagnostic patients were found to be impaired when asked to choose the one out of two faces that is looking directly at them (Campbell, Heywood, Cowey, Regard, & Landis, 1990) suggesting some kind of interrelation of the processing of eye gaze and identity (a finding which is not in line with the model proposed by Bruce & Young, 1986, assuming identification processes and the analysis of changeable features to happen independently and in parallel).

Suggesting further interactions of gaze processing with identity recognition and personality judgements, Bayliss and Tipper (2006) showed in a cueing paradigm that face identities which had always been presented as predictive and valid cues (i.e. always gazing at the target location) were judged more trustworthy than face identities presented as predictive but invalid cues (i.e. always gazing at the non-target location). Similarly, it has been shown that smiling faces were judged more attractive when gazing directly at the observer whereas neutral faces received higher ratings of attractiveness when showing averted gaze (Conway, Jones, DeBruine, & Little, 2008; Jones, DeBruine, Little, Conway, & Feinberg, 2006; see also Ganel, Goshen-Gottstein, & Goodale, 2005). Finally, indicating strong interactions between the processing of eye gaze and emotion, Adams and Kleck (2003) found that direct gaze facilitates the processing of approach-oriented emotions (i.e. anger and joy) whereas averted gaze facilitates the perception of avoidance-oriented emotions (i.e. fear and sadness). It has to be considered, however, that Bindemann, Burton, and Langton (2008) could not replicate these findings in an extensive series of experiments. The question of whether the perception of eye gaze direction, approach-oriented, and avoidance-oriented emotions interact is therefore not resolved yet.

Considering the importance of information contained in human eye gaze, it is an interesting question *how* we actually perceive the direction of gaze. It is likely that we are only able to extract this wealth of information from the eye region because it evolved in a special way, making human eyes unique with regard to their morphology. Kobayashi and Kohshima (1997; Kobayashi & Kohshima, 2001) pointed out that whereas most animals' eyes consist of a dark sclera (usually of similar colour as the surrounding skin) and a dark iris and pupil, human eyes have a large, exposed and bright sclera which is even lighter than the colour of the skin and sets a strong contrast to the darker iris and pupil. This strong light/dark contrast makes the accurate perception of human eye gaze so much easier than that of other species (see Figure 3, for an example). The unique morphology of the human eye therefore seems to provide the basis for human non-verbal communication using eye gaze signals which is less pronounced in other primates (Kobayashi & Kohshima, 1997; Kobayashi & Kohshima, 2001).

Figure 3: Orangutan (left) and human eye (right) as an illustration of the unique morphology of human eyes described by Kobayashi and Kohshima (1997; Kobayashi and Kohshima, 2001). Of special importance are the differences in the iris/sclera contrast and the eccentricity of the sclera, both of which are larger in human eyes as compared to other primates. Pictures taken from Kobayashi and Kohshima, 2001.

Initially, the geometric (or configural) information contained in the eye region (i.e. the relative position of the angle between the eyelids to the circle formed by the iris) was considered to be the key factor in gaze perception (Anstis, Mayhew, & Morley, 1969; Langton, Watt, & Bruce, 2000). As in studies on general face perception the relative contribution of configural information has been investigated by rotating the stimulus. The results are inconsistent: Jenkins and Langton (2003) found sensitivity to gaze direction to be severely affected by eye inversion, independent of the orientation of the face context. They concluded that eye gaze processing in normal, upright orientation relies on configural processing (see also Schwaninger, Lobmaier, & Fischer, 2005). Tipples (2005), however, investigated the attentional orienting to eye gaze and found reliable gaze cueing effects from both upright and inverted faces and concluded local, part-based information to be critical for the perception of and orienting to eye gaze. Finally, Campbell et al. (1990) found that face inversion only impaired participants' ability to discriminate small deviations of the eyes whereas larger deviations could still be discriminated at high levels of accuracy.

There is accumulating evidence that luminance information also plays an important role in the perception of eye gaze direction. The iris-sclera ratio and -contrast have been identified as important factors in gaze perception (Ando, 2002; Ando, 2004; Ricciardelli, Baylis, & Driver, 2000; Tipples, 2005). Sinha (2000) presented the so-called 'Bogart-illusion' which is characterised by a reversal of the perceived gaze direction through contrast negation of a photograph of the famous actor. More precisely, the contrast negation of a photograph of a person looking to the left makes the observer perceive the person as looking to the right (see Figure 4). Sinha (2000) therefore proposed that human eye gaze perception is guided by a simple rule of thumb which defines the darkest part of the eye as the iris position (and hence the direction of eye gaze). Similarly, Ando (2002) found that after darkening one side of the sclera a substantial shift of the perceived gaze direction towards the darkened side takes place (for an illustration, see Figure 4). Both Sinha (2000) and Ando (2002) concluded that low-level analysis of the luminance distribution within the eye region is an important mechanism in the computation of gaze direction.

The recent publication of a new visual illusion seems to integrate the contribution of both configural and luminance aspects. Jenkins (2007) presented the picture of a woman whose eye gaze is perceived as being directed to the left when viewed at a close range. From further away, however, the same person is perceived as gazing to the right (see Figure 4). In Jenkins' stimulus, the darkest parts of the eyes which were located close to the right canthi were only then perceived as the iris when the image was viewed from some distance. From a closer distance, however, the brighter parts near the left canthi of the eyes in combination with their roundish contour (not detectable from the distance) lead to the impression of an iris gazing to the left. To sum up, it can be concluded that both configural (i.e. geometrical) and featural (e.g. luminance) aspects within the eye region seem to be involved in the perception of gaze direction.

Several studies have investigated the neural basis of eye gaze processing. In single-cell recordings, cells selectively responding to direct and averted gaze directions have been identified in the macaque superior temporal sulcus (Perrett et al., 1985; Perrett, Hietanen, Oram, & Benson, 1992). Consistently, bilateral removal of the STS in monkeys led to a loss of the ability to discriminate between direct and averted gaze (Campbell et al., 1990).

Figure 4: Left panel, top row: ‘Bogart illusion’ first described by Sinha (2000). Contrast negation of the original image leads to a change in the perceived gaze direction. Left panel, bottom row: ‘Bloodshot illusion’ (Ando, 2002). Darkening one side of the sclera leads to a shift of the perceived gaze direction towards the darkened side. Right panel: Gaze direction illusion as described by Jenkins (2007). All illustrations copied from the original papers.

Functional imaging studies suggest that regions within the superior temporal sulcus are also involved in gaze processing in humans (Hoffman & Haxby, 2000), probably especially when observing eye *movements* in others (Pelphrey, Viola, & McCarthy, 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Findings that regions involved in identity recognition and eye gaze perception are functionally dissociable (Hoffman & Haxby, 2000) are in line with the Haxby model on face perception (Haxby et al., 2000) assuming an analysis of the invariant aspects of faces (e.g. identity) in the fusiform gyrus, whereas eye gaze information is assumed to be mainly processed in the superior temporal sulcus and the intraparietal sulcus. Further, Calder et al. (2002) showed in a positron emission tomography (PET) study that eye gaze processing leads to activation in the medial prefrontal cortex (MPF), a region which has earlier been found to be involved in the attributions of aims and intentions of others (Baron-Cohen, 2001). Some studies also found the amygdala to be involved in gaze processing, with activity in the right amygdala being reported to increase when an observer is confronted with direct gaze (Kawashima et al., 1999). In line with this study and evidence that right amygdala activity is enhanced when participants are actively monitoring for emotional gaze events in others (Hooker et al., 2003), the amygdala has been suggested to be involved in directing our attention towards the eye and mouth regions of a face (Benuzzi et al., 2007).

In addition to imaging studies investigating the brain structures involved in eye gaze perception, electrophysiological studies have been conducted in order to evaluate the ERP correlates of gaze perception. There is some evidence that the perception of eye gaze is mainly reflected in the occipitotemporal N170 component, with some studies finding that the amplitude and latency evoked by isolated eye stimuli are enhanced relative to the presentation of full faces (Bentin et al., 1996; Jemel, George, Chaby, Fiori, & Renault, 1999; Itier, Latinus, & Taylor, 2006; but see Eimer, 1998). Further stressing the sensitivity of the N170 for eye information, it was found that faces with eyes closed evoked a significantly delayed N170 compared to both averted and direct gaze (Taylor, Itier, Allison, & Edmonds, 2001). Finally, some experiments suggest that the N170 face inversion effect is mainly due to inversion of the eye region (Doi, Sawada, & Masataka, 2007; Itier et al., 2006). Together, these findings propose that the N170 might reflect the activity of an eye detector (Bentin et al., 1996).

With regard to the effects of gaze direction processing on electrophysiological components, several studies found the N170 amplitude to be larger in response to eye aversion than in response to eyes gazing directly at the observer (Itier, Alain, Kovacevic, & McIntosh, 2007a; Puce, Smith, & Allison, 2000; Watanabe, Miki, & Kakigi, 2002). Investigating the interrelation of the perception of head orientation and gaze direction, Itier et al (2007a) specified that the finding of larger N170 amplitudes for averted than for direct gaze seems to be restricted to front-view faces as it could not be found for ¾-view faces. In a later time window of about 400 - 600 ms the authors found larger amplitudes in response to direct gaze – irrespective of the head orientation – and concluded that this stage might reflect the final outcome of gaze processing.

To sum up, the perception of eye gaze has been shown to be a very important aspect of social perception and cognition. Perceiving information from the eye region of others improves our understanding of their emotions, intentions, and aims and therefore enhances our ability to act appropriately in social situations. Further, the precise perception of the gaze direction of others has been shown to influence the focus of our own attention. It has been revealed that both luminance and geometrical information are processed in order to infer the direction of gaze of another person. ERP studies provided evidence that the perception of eyes and eye gaze is mainly reflected in the N170 component. Finally, the STS region, the medial prefrontal cortex, and the amygdala seem to be important neural structures enabling us to process and interpret the direction of gaze of others.

2.1.3 Gender Perception

Adults can easily discriminate between male and female human faces even when pictures are of low quality (Cellerino, Borghetti, & Sartucci, 2004). Young children, however, despite having an inborn preference for face stimuli (Johnson et al., 1991) fail to make this distinction before the age of about five to eight months (Fagan, 1967; Fagan, 1974). Even after that age, young children show a great asymmetry in processing faces of both genders as they are more fluent in processing female than male faces (Ramsey, Langlois, & Marti, 2005; Ramsey-Rennels & Langlois, 2006). These findings concerning gender discrimination abilities in infants strongly suggest that our proficiency to extract the gender of a face develops over time due to accumulating visual experiences with male and female faces. In adulthood, the identification of the gender of a face happens faster than its recognition (Bruce, 1986) and is an important basis of our social interactions with known and unknown people.

Several studies have been conducted in order to understand the physical differences between male and female faces. First, the information related to the colour (Hill, Bruce, & Akamatsu, 1995), brightness, and luminance of faces seems to play an important role for gender discrimination. Male skin tends to be darker than female skin (Frost, 1988) and the distributions of luminance across the face seems to differ between males and females: darker eyes and mouth surrounded by brighter skin parts are naturally greater in women than men and a face can therefore be made more feminine or masculine by changing this luminance difference (Russell, 2003).

Related to these aspects of physical stimulus properties, Cellerino et al. (2004) measured the minimum information necessary for correct gender classification and found that better picture quality was needed for a correct classification of female faces as compared to a correct classification of male faces, i.e. male faces seem to be categorised more easily than female faces. Second, some featural aspects of faces such as the eye region and the facial outline (Brown & Perrett, 1993; O'Toole et al., 1998; Yamaguchi, Hirukawa, & Kanazawa, 1995), the size of the nose, and the prominence of the eyebrows (Campbell, Benson, Wallace, Doesbergh, & Coleman, 1999; Enlow, 1982) have been found to differ systematically between the two sexes. Third, in studies concerning the structural differences between male and female faces it has been found that the distance between the brow and the upper eyelid is one of the most reliable structural cues to gender in static faces (Brown & Perrett, 1993). This distance is typically smaller for men than for women. Related to this, different head movements and postures can influence the ease with which we determine the gender of faces. For example, male faces with lowered brows are more accurately and quickly categorised (Campbell et al., 1999) whereas male faces looking down and therefore increasing the perceived brow-lid distance have been shown to be rated more feminine than the same faces looking directly at the observer (Campbell, Wallace, & Benson, 1996).

Further, high levels of facial attractiveness have been shown to facilitate the speed of gender classification of both male and female faces (Hoss, Ramsey, Griffin, & Langlois, 2005), a finding which is in line with the assumption that the level of perceived attractiveness is highly correlated to the extent to which features and spatial aspects in faces are prototypical for their respective gender (Langlois & Roggman, 1990; Rhodes & Tremewan, 1996). A study by Perrett et al. (1998), however, found a different relationship between the gender-prototypicality of faces and their perceived attractiveness. Irrespective of their own gender, participants judged feminised versions of both female and male faces as more attractive than female and male average faces, respectively. Additionally, enhancing masculine facial characteristics of male faces was found to lead to decreased rankings of perceived warmth, emotionality, honesty, cooperativeness, and quality as a parent compared to average male faces. Together, these findings stress the strong interrelation between the evaluation of attractiveness and mating behaviour. Humans seem to prefer facial features that are associated with care-giving, honest, and responsible behaviour.

Apart from these purely face-driven aspects of gender discrimination, information from other modalities has been shown to influence the decision of whether a presented face is male or female. In an auditory-visual cross-modal study, Smith, Grabowecky, and Suzuki (2007) found that androgynous faces were more likely to be judged as male when presented together with pure tones in the male fundamental speaking frequency range and more likely to be judged as female when presented with pure tones in the range of female fundamental speaking frequency. Similarly, it has been shown that male participants perceive faces to be more masculine when simultaneously exposed to the smell of male sex hormones such as steroids (Kovács et al., 2004).

Until now, there have been only a few studies examining the neural structures and processes underlying gender perception. A comparison of the event-related potentials evoked by the presentation of human hands and faces requiring different degrees of gender discrimination revealed that the degree of gender processing had no effect on N170 amplitude or latency at occipitotemporal electrodes (Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000). The processing of face gender, however, affected the ERPs measured at more anterior scalp locations in the N170 time range (145 -185 ms). At these electrode locations, trials requiring a gender decision were characterised by larger amplitudes than trials that did not ask for a gender decision. In line with the Haxby model on face perception (Haxby et al., 2000), Mouchetant-Rostaing et al. (2000) concluded that the neural mechanisms involved in the structural encoding of faces have to be different from those involved in the extraction of gender-related facial features (but see Ganel & Goshen-Gottstein, 2002).

In a PET study on face recognition and gender discrimination (Sergent, Ohta, & MacDonald, 1992) the right cuneus, the right inferior occipital and occipitotemporal gyrus, the right lateral occipital gyrus, and the left middle occipital gyrus were found to be involved in a gender discrimination task. This dominance of the right hemisphere in gender perception was also reflected in the results of a visual hemifield study by the same authors, showing that face-gender discrimination is faster when stimuli are presented to the left visual field (Sergent et al., 1992).

Interestingly, there seem to be differences in the perception of face gender between male and female participants. In general, women have been reported to outperform men in both face recognition and gender discrimination tasks. These gender differences have been suggested to at least partially result from motivational differences in task involvement in male and female participants (Sporer, 1991). However, such motivational differences do not seem to be able to explain all gender differences. In gender discrimination tasks, for example, the better performance of female participants has usually been found to result from their greater efficiency in detecting female faces, whereas there were no differences in the ability to detect male faces (Cellerino et al., 2004; Lewin & Herlitz, 2002). Several studies have reported an *own-gender bias*, i.e. both males and females were found to be more efficient in recognising faces of their own gender than faces of the other gender (Cellerino et al., 2004; Lewin & Herlitz, 2002; Wright & Sladden, 2003), an effect which has been attributed to the development of visual experiences from early childhood on (Ramsey et al., 2005). Further evidence for differences in gender discrimination in male and female participants was reported by Fischer et al. (2004). In an fMRI study, they compared brain responses to male and female stimuli in male and female participants. During exposure to female faces male participants showed an increased fMRI signal in the left amygdala and anterior temporal regions which was absent in female participants when presented with male face stimuli. The authors concluded that the amygdala and the anterior temporal cortex may play a role in the perception of gender discriminating social signals in faces, especially in men.

Apart from facial images, gender can also be determined from different sources of information. One example is the acoustic perception of a person's gender from listening to his or her voice (Fellowes, Remez, & Rubin, 1997; Lass, Almerino, Jordan, & Walsh, 1980; Lass, Hughes, Bowyer, Waters, & Bourne, 1976). A recent study has shown that the perception of gender from voices can be biased as a consequence of adaptation (Schweinberger et al., 2008).

A second example of a possible source for gender perception is the visual information contained in the human gait pattern (Barclay, Cutting, & Kozlowski, 1978; Kozlowski & Cutting, 1977). In studies investigating the perception of this kind of biological motion stimuli are usually derived from attaching lights to the major joints of the body. Only these lights, so-called point light walkers (PLW), are shown to participants to selectively investigate motion perception. The information contained in these lights alone has been shown to be sufficient for correct gender discrimination (Barclay et al., 1978; Kozlowski & Cutting, 1977). In analogy to faces and voices, the prolonged exposition to the biological motion of male or female walkers has recently been shown to also induce opposite gender aftereffects (Jordan, Fallah, & Stoner, 2006) as will be reported in chapter 2.2.4 in more detail.

To summarise, different sources of information such as faces, voices, or the movements of a person allow for a correct categorisation of his or her gender. In faces, luminance, featural, as well as configural information seems to contribute to accurate gender perception. Differences in the processing of facial gender in early childhood and the *own-gender bias* observed in adults underline the influence of visual experience on the development of gender representations. Gender discrimination has been shown to affect ERPs measured in the time range of the N170, however, at more anterior scalp locations. Imaging studies suggest structures such as the cuneus, the inferior occipital and occipitotemporal gyri predominantly of the right hemisphere to be involved in gender perception.

2.2 Perceptual Adaptation

Our perceptual systems have evolved over millions of years, providing us now with highly efficient sensory modalities which are specialised for the perception of our environment. But changes in the human perceptual system have not only been of great importance with regard to phylogenesis – even in our everyday lives we rely on the flexibility of our perceptual system. One of the mechanisms allowing for a flexible interaction of our visual representations and the environment is perceptual adaptation. Neural adaptation is a mechanism by which specific neural responses decrease after prolonged stimulation. Traditionally, the effects of adaptation and their neural correlates have been investigated for low levels of visual perception or for relatively simple stimulus properties, such as motion or colour. In the last few years, however, adaptation effects have also been reported for the high-level perception of complex visual patterns such as human faces.

After a short introduction into the principles of adaptation using the example of simple stimulus properties (2.2.1), findings of face-related high-level adaptation will be reported in greater detail (2.2.2). Following an overview of the findings on the specific effects of adaptation to eye gaze (2.2.3) and gender information in faces (2.2.4), the aims of the studies presented in the current thesis will be outlined (2.2.5).

2.2.1 Adaptation to simple stimulus attributes

Adaptation is one of the fundamental properties of the neurons involved in the processing of our perceptions. It occurs when a perceptual system changes its processing characteristics due to the current information. According to Barlow's hypothesis of efficient coding, neural systems which have finite possibilities to transfer information therefore obtain optimally efficient coding strategies by recalibrating their response patterns to the stimulus properties they are typically confronted with (Barlow, 1961). As a consequence, perceptual sensitivities are adjusted to the set of environmental stimuli, a process which has been described as 'fitting the mind to the world' (Clifford & Rhodes, 2005). The systematic investigation of the aftereffects of adaptation can therefore provide a detailed insight into the neural coding and the distinct representations of sensory information. Thanks to this completely non-invasive but detailed view into the functioning of the human brain, psychophysical aftereffects have been termed the *psychologist's microelectrode* (Frisby, 1980). Visual adaptation, i.e. adaptation within neural entities involved in visual perception, has therefore long been investigated in order to gain information about the processing mechanisms of the human visual system. Traditionally, these aftereffects have been studied and reported for early stages of processing and for relatively simple stimulus characteristics such as luminance, contrast (e.g. Chen, Zhou, Gong, & Liang, 2005), colour, or motion (e.g. Antal et al., 2004).

Here, the basic principles of adaptation will be explained using the example of the motion aftereffect (MAE) which was first described by Aristotle (*Parva Naturalia*) and which is probably among the most popular and most extensively investigated examples of visual adaptation to relatively simple stimulus properties. Here, the prolonged viewing of a downward-moving stimulus subsequently leads to the illusionary perception of an upward motion in a static image (see Anstis, Verstraten & Mather, 1998, for a review). This phenomenon has been explained as being the result of a disequilibrium between motion detectors tuned to opposite directions, with neural fatigue (Barlow & Hill, 1963) and reciprocal inhibition processes (Culham et al., 1999; Tootell et al., 1995) being discussed as possible underlying neural mechanisms. The prolonged viewing of downward motion has been assumed to lead to habituation of the neural channels selectively coding this property. Due to this selective habituation, the offset of the moving stimulus leads to a strong decrease in the adapted channels' activity, which therefore drops below baseline activity. The resulting higher level of activity in the unadapted channel (coding upward motion) relative to the remaining activity in the adapted channel (coding downward motion) therefore leads to the illusionary perception of upward motion in a static image.

The observation of this MAE therefore revealed detailed and non-invasive insight into the organisation of the neural system processing vertical motion - with strong evidence for one subsystem detecting upward motion and a second subsystem detecting downward motion. There is empirical evidence for the correlation of behavioural aftereffects with a reduction in neural activity in cell populations selectively responding to a certain characteristic of the respective stimulus (Grill-Spector & Malach, 2001). However, the exact process underlying this decrease of neural sensitivity is not yet resolved. It might result from a general decrease of amplitude of stimulus-responsive neurons, from a ‘sharpening’ of sensitivity in terms of fewer responding neurons, or a shortening of the duration of neural activity (Grill-Spector, Henson, & Martin, 2006a). Whatever may be the exact underlying neural mechanisms, it is evident that an increased sensitivity to stimuli with different (i.e. unadapted) characteristics is one of the major consequences of perceptual adaptation, therefore providing a mechanism for *‘novelty detection’*.

The timing parameters of low-level adaptation have been widely investigated. In general, three important variables influencing the time-course have to be distinguished. These aspects are the presentation duration of the adaptor, the presentation duration of the test stimulus, and the time interval between the adaptor and test stimulus. Empirical findings vary considerably across adapted visual properties, methodological details of the respective experiments, and even across participants. However, generally speaking, the strength of most aftereffects increases as a function of adaptation time and decrease as a function of presentation duration of the test stimulus. The duration of motion aftereffects was reported to increase as a power function of the presentation time of the adaptation stimulus, while the decline was described by an exponential decay function (e.g. Hershenson, 1989; Hershenson, 1993; see also Petersik, 2002, for a report of an exponential decay for three-dimensional MAEs).

Even if the reasons described above make it difficult to state a universal value as the ’typical’ duration of low-level aftereffects, it might be interesting to consider the variety of timing parameters observed in studies on different adaptation effects. Investigating the effects of varying adaptation durations between 30 s and 15 min, Hershenson (1989) observed that motion aftereffects decayed after only 17 to 75 s. Following adaptation to prisms, however, aftereffects have been found to be characterised by a very slow decay rate. A recent study described the aftereffects of a single 75 min prism adaptation session to be still measurable after 7 days (Hatada, Miall, & Rossetti, 2006).

Recently, visual aftereffects have also been reported for complex visual patterns in high-level vision, especially in face perception (Webster & Maclin, 1999). These findings build the framework for the experiments presented here and will be reported in detail in the following sections. Altogether, studies investigating adaptation effects of higher-level perceptual processes suggest that adaptation may routinely influence perception in normal viewing and is not just a phenomenon measured in laboratories (Webster & Maclin, 1999).

2.2.2 High-level adaptation in face perception

While adaptation to simple stimulus attributes has been known for literally thousands of years, it has been a striking novel discovery within the last few years that adaptive recalibration is also of central importance for the perception of very complex visual stimuli such as human faces. The technical progress over the last decades has been a major prerequisite of these studies, as new stimulus editing techniques such as image *morphing* provided access to high-quality, photorealistic images with well-controlled features and a very fine-graded variation of specific stimulus aspects. It is possible, for instance, to derive a continuum of images from a pair of photographs, e.g. a male and a female face, which contains different levels of gender ambiguity and a completely gender-ambiguous face as the centre.

The first study reporting visual aftereffects in face perception was published by Webster and MacLin (1999). They reported a so-called face distortion aftereffect (FDAE) which is a figural adaptation effect in the perception of face configurations. They found that adaptation to distorted (e.g. contracted) faces led to an altered perception of normal faces in the direction opposite to adaptation (e.g. expanded). Similar high-level adaptation resulting in contrastive aftereffects has also been reported for other face-related processes such as the perception of identity (Leopold, O’Toole, Vetter, & Blanz, 2001), gender (Bestelmeyer et al., 2008; Kovács et al., 2006; Webster, Kaping, Mizokami, & Duhamel, 2004), eye gaze (Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006), viewpoint (Fang, Ijichi, & He, 2007), ethnicity

(Webster, Kaping, Mizokami, & Duhamel, 2004), emotional expression (Butler, Oruc, Fox, & Barton, 2008; Fox & Barton, 2007; Webster et al., 2004), and audiovisual speech integration (Bertelson, Vroomen, & de Gelder, 2003; Vroomen, van Linden, de Gelder, & Bertelson, 2007). These-high level visual aftereffects have been shown to be to a large extent size invariant (e.g. Zhao & Chubb, 2001), suggesting that they do not mainly reflect adaptation to single features on low levels of visual processing.

Similar to the investigation of adaptation effects for simple stimulus characteristics, figural high-level adaptation experiments can provide a valuable insight into the mechanisms and functional organisation of face perception. Webster and MacLin (1999), for example, reported the FDAE to be asymmetric, i.e. adaptation to distorted but not to undistorted (‘normal’) faces showed a clear effect on the perception of subsequently presented test faces. This is in line with the ‘face-space’ theory (Valentine, 1991) which suggests face representations as being organised in a multi-dimensional space with an average face prototype as the centre (see also Leopold et al., 2001).

Rhodes et al. (2004) provided further insight into the organisation of face representations showing orientation-dependent aftereffects in face perception. The authors found that opposite face distortion aftereffects could be simultaneously induced for upright and inverted faces. Adaptation to upright faces with contracted internal features and inverted faces with expanded internal features led to a simultaneous shift of the perceived most normal looking distortion to a more contracted version in upright and to a more expanded version in inverted faces. Rhodes et al. (2004) further reported equivalent orientation-dependent aftereffects for face gender, i.e. simultaneous adaptation to upright male faces and inverted female faces led to classifications of gender-ambiguous faces as more female when presented in upright orientation and as more male when presented in inverted orientation. These findings are in line with several other studies reporting weak transfer of adaptation effects across orientations (Robbins, McKone, & Edwards, 2007; Watson & Clifford, 2003; Webster & Maclin, 1999) supporting the idea that separate mechanisms and distinct neural populations selectively code upright and inverted faces.

A recent study revealed further simultaneous category-contingent eye spacing aftereffects for different ethnicities (i.e. male European vs. male African faces), ages (i.e. male adult vs. male infant faces), and species (human vs. monkey faces) suggesting that these different categories are also represented in functionally distinct neural populations (Little, DeBruine, Jones, & Waitt, 2008).

Fox and Barton (2007) investigated the aftereffects of adaptation to emotional expressions within and across identities. They found emotional aftereffects to be most pronounced for within-identity adaptation but they also reported that emotion adaptation produced weaker but significant aftereffects on different identities. These data therefore provided further insight into the neural representations of emotional expressions in suggesting that there are both identity-specific and general identity-invariant representations of expressions.

Related to the findings of face distortion aftereffects, several studies reported face identity aftereffects (FIAEs; e.g. Leopold, O'Toole, Vetter, & Blanz, 2001). That is, the exposure to an individual face systematically biased the perceived identity of a subsequently presented different face. Using a morphing technique, Leopold et al. (2001) created a complex set of face stimuli. They generated the image of an average face by morphing 100 male and 100 female faces and then created anti-faces by morphing images of individual faces towards this average face and beyond it. This procedure resulted in face/anti-face pairs, i.e. for each individual veridical image a second face image was created that deviated from the average face in a manner opposite to the veridical. For instance, when “Henry” was characterised by a large eye distance, thick eyebrows, a broad nose, and a large mouth, the resulting ‘Anti-Henri’ would be characterised by a small eye distance, slim eye brows, a narrow nose and a small mouth (see Figure 5).

Using these stimuli, Leopold et al. (2001) found that adaptation to the anti-face of a certain individual subsequently led to an increased sensitivity to perceiving the original identity of the same person. For example, performance in identifying the average face as a certain identity moved from chance performance in baseline trials to greater than 60% ‘correct’ identification. This means that adaptation to an anti-face of a certain identity subsequently makes an average face look like this person. By contrast, the authors showed that test stimuli that were on a different identity trajectory than the anti-face (i.e. not the veridical faces used to create that anti-face) were less likely to be identified correctly after adaptation.

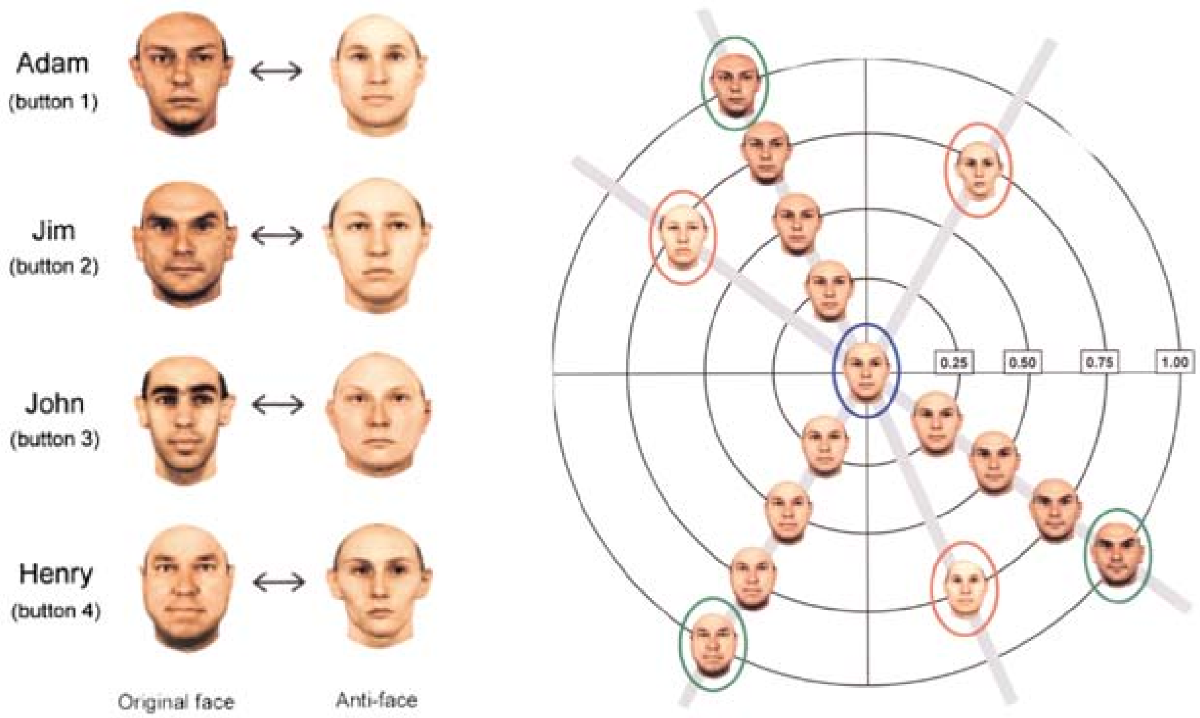


Figure 5: Examples of the stimulus set used by Leopold et al. (2001). Left panel: Face/anti-face pairs of four different identities. Each anti-face (red circles in right panel) differs from the average face (blue-circled face at the centre of the right panel) in an opposite manner to the original face (green circles). Figure copied from Leopold et al (2001).

These effects were found for both upright and inverted stimuli, with adaptation and test faces always presented in the same orientation, suggesting that the mechanisms underlying both upright and inverted face recognition are recalibrated in an adaptive manner (see also Kovács, Zimmer, Harza, Antal, & Vidnyanszky, 2005). This finding is of special importance as it revealed similarities in the response properties of the distinct neural mechanisms that have been assumed to be applied in the processing of upright and inverted faces (see chapter 2.1.1).

A similar study (Jiang, Blanz, & O'Toole, 2006) revealed that identity adaptation could also be observed with adaptation and test stimuli containing either only facial shape *or* surface reflection information indicating that both face-shape and reflectance can carry information about the identity of a face. Further, Jiang et al. (2006) found identity adaptation effects to transfer across large changes in viewpoint, in this case a rotation of the stimulus by 30°, underlining the idea that face recognition is very robust to variations in changeable aspects and therefore in line with both the Bruce and Young (1986) and the Haxby model (2000) of face perception.

Some studies have examined the temporal aspects of face adaptation: In an informal report, Leopold et al. (2001) mentioned having tested the robustness of FIAEs to varying delays between adaptation and test stimulus of 150, 300, 600, 1200, and 2400 ms. They found adaptation effects to be reduced for intervals longer than 300 ms but to stay at a significant level up to the longest delay of 2400 ms. Leopold, Rhodes, Müller, and Jeffery (2005; see also Rhodes, Jeffery, Clifford, & Leopold, 2007) explored the dynamics of face-adaptation and compared them to those of simple after-effects which are known to be influenced by both the duration of adaptation and the presentation duration of the test stimulus. The authors tested the dependence of the FIAE on a wide range of durations of the adapting and test stimulus. In line with traditional aftereffects they found the FIAE to increase as a function of adaptation time and to decrease as a function of test duration, i.e. presentation period of the test stimulus. A major limitation of this study is, however, that the effect of different inter-stimulus intervals between the presentation of the adaptation and test stimulus has not been examined. Therefore, there is no further information concerning the long-term effects of high-level adaptation in face perception apart from that they survive the relatively short interval of 2.4 s between adaptor and test stimulus presentation (Leopold, O’Toole, Vetter, & Blanz, 2001; but see Carbon and Leder (2006) for an informal report of a face distortion aftereffect lasting over 24 hours in the perception of a painting). Examining the effects of adaptation duration on face viewpoint aftereffects, Fang, Murray, and He (2007) revealed differential effects of long-term adaptation (i.e. 5 s) and short-term adaptation (i.e. 300 ms) with long-term adaptation effects being view-point specific and short-term adaptation effects being viewpoint-invariant. An ERP study on gender adaptation similarly reported differential effects of the duration of adaptation, however, this study investigated *position* specificity of adaptation effects, i.e. the dependence of adaptation effects on identical presentation locations of adaptor and test stimuli (Kovács, Zimmer, Harza, & Vidnyanszky, 2007). This study will be reported in greater detail in chapter 2.2.4.

Further, the neural correlates of behavioural aftereffects have been investigated using fMRI-adaptation (Grill-Spector & Malach, 2001). The regional specialisation of selective cell populations can be inferred from this method with greater specificity than from the subtractive methodology conventionally used in imaging studies (Winston, Henson, Fine-Goulden, & Dolan, 2004). The logic of the method is based on the assumption that neurons specifically responding to distinct information of a stimulus will habituate when this aspect is repeated. Therefore, after sequential presentations of stimuli repeating a certain aspect the neuronal population that is sensitive to that information is adapted, leading to a decreased blood-oxygen level dependent (BOLD) signal in that region compared to an unrepeated presentation of that aspect (Grill-Spector et al., 2006a; Sawamura, Orban, & Vogels, 2006). If a change in one stimulus property subsequently leads to a recovery from adaptation, the underlying brain mechanisms are assumed to be sensitive to that stimulus property. The application of this technique allows for a deeper insight into the neural basis of adaptation effects and provided strong evidence for the assumed dissociation between the neural representation of identity and changeable aspects of human faces (Furl, van Rijsbergen, Treves, & Dolan, 2007; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston et al., 2004) that was proposed by Bruce and Young (1986) and Haxby et al. (2000).

Using fMRI adaptation, Löffler and colleagues (2005) were able to specify the way faces are mentally represented and identified (Löffler, Yourganov, Wilkinson, & Wilson, 2005). Consistent with the concept of a multidimensional face space (Valentine, 1991), they found that neurons in the fusiform face area code facial identity in terms of deviance from a prototypical (i.e. average) face. Using the same technique, Andrews and Ewbank (2004) further found that the fusiform gyrus shows weaker response to repeated presentations of the same face as compared to different faces – independent of the stimulus size but sensitive to different viewpoints of the face – further stressing the role of the fusiform gyrus in the identification of individual faces. In contrast, in the STS they found larger responses to the same face shown from different viewpoints/with different expressions compared to different faces viewed from different viewpoints/with different expressions, suggesting that this region is responsible for the analysis of the changeable aspects of faces important in social communications (Haxby et al., 2000).

However, due to the low temporal resolution of fMRI the reported adaptation effects reflect the neuronal activity of several seconds, making it difficult to decide whether the neural habituation measured is really due to perceptual or to later processes (Harris & Nakayama, 2007). To fully understand the nature of face adaptation effects, it is therefore important to also investigate their electrophysiological correlates with the excellent temporal resolution of electroencephalography (EEG) or magnetoencephalography (MEG). The first studies that systematically investigated the electrophysiological correlates of face adaptation (Kovács et al., 2005; Kovács et al., 2006) found effects of adaptation on the amplitude of the N170 component in a gender adaptation paradigm (as will be reported in greater detail in section 2.2.4). Similarly, later studies also confirmed the sensitivity of the M170 to face adaptation (Ewbank, Smith, Hancock, & Andrews, 2008; Harris & Nakayama, 2007; Harris & Nakayama, 2008). Together, these studies clearly indicate the perceptual nature of the investigated adaptation effects.

2.2.3 Gaze Adaptation

Two studies published at the same time independently reported negative aftereffects following adaptation to eye gaze direction (Jenkins et al., 2006; Seyama & Nagayama, 2006). Jenkins et al. (2006) conducted a series of three experiments in order to investigate the functional organisation of the human gaze processing system. They hypothesised that if distinct cell populations selectively code different gaze directions in humans it should be possible to selectively adapt these populations resulting in different aftereffects following adaptation to left and right gaze direction, respectively. In their main experiment, they indeed found that adaptation to consistent strong gaze deviations to the left or to the right produced an illusion that eliminated observers' perception of smaller gaze deviations in the adapted direction. Testing the baseline ability to correctly distinguish between gaze directions, they found that participants were highly accurate in correctly identifying direct gaze (~87% correct) or eye gaze directed 10° to the left or right (~98 % correct) and less accurate in discerning gaze that was averted by only 5° to the left or right (~71% correct). After adaptation to gaze averted 25° to left or right direction the ability to subsequently perceive gaze directed to that side was nearly eliminated (more than 80% direct responses for both left and right stimuli following adaptation to left and right gaze direction, respectively, see Figure 6 for an overview of the results). That is, following adaptation observers showed a striking tendency to judge gaze in the adapted direction as looking directly at them. Responses to direct gaze, however, were not significantly affected by adaptation and the authors stated that there was no loss of sensitivity to gaze that was directed to the unadapted side.

These findings clearly suggest that distinct cell populations code different directions of gaze in humans. To rule out the possibility that the adaptation effects found in this first experiment merely reflected low-level visual adaptation, Jenkins et al. (2006) ran two variations of the experiment in which retinotopic mapping between the adaptation and test stimuli was severely disrupted by changes in the size (Experiment 2a) or head orientation (Experiment 2b) of the adaptation stimuli. Despite these changes, the results were remarkably similar to those of Experiment 1 (see Figure 6) and therefore excluded the possibility that the findings of the first experiment were due to low-level adaptation processes. There were slight differences compared to the results of the first study, however, as in Experiment 2b, using adaptation stimuli with a different head orientation than the test stimuli, sensitivity for gaze directed 5° to the unadapted side was slightly improved after adaptation and subjects showed a tendency to judge direct gaze as pointing in the unadapted direction.

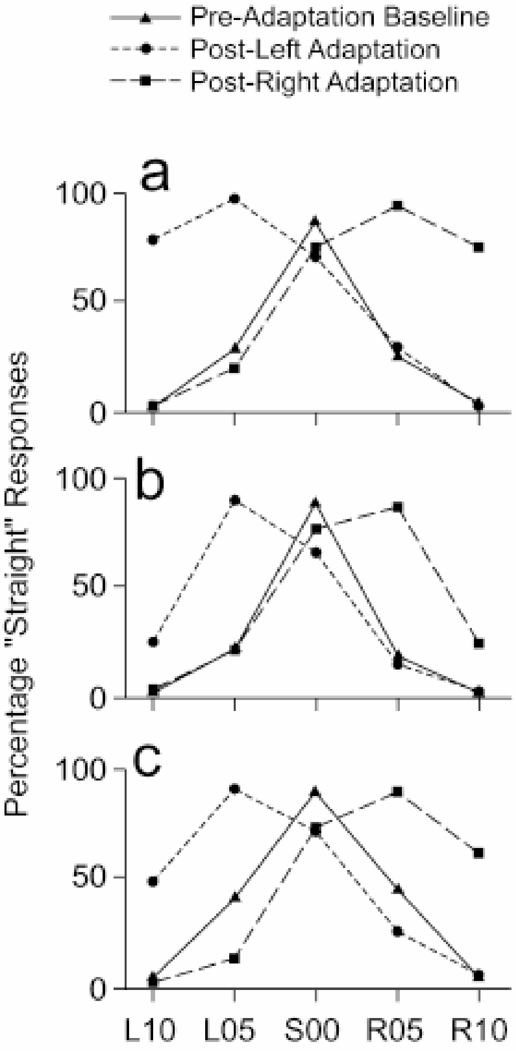


Figure 6: Results of the eye gaze adaptation experiments conducted by Jenkins, Beaver, and Calder (2006). Percentages of “direct” responses (y-axis) obtained in the pre-adaptation baseline (solid lines), following adaptation to left (dotted line) and right gaze direction (dashed line) in response to test stimuli of the five different gaze directions (x-axis). Abbreviations on the x-axis L10, L05, S00, R05, and R10 represent test stimuli gazing 10° left, 5° left, directly at the observer, 5° right, and 10° right, respectively. a) Results of Experiment 1, b) Results of Experiment 2a, c) Results of Experiment 2b. Figure copied from Jenkins et al. (2006).

Finally, Jenkins et al. (2006) conducted a third experiment to examine whether the observed aftereffects were specific for human eye gaze or whether gaze adaptation influenced spatial estimations more generally. In this experiment, participants were again adapted to gaze averted by 25° from direct gaze but were then tested on a landmark task during which they had to decide whether a vertical bar crossed a horizontal line centrally or left or right from the centre. Importantly, deviations of the vertical bar from the centre physically corresponded to the magnitude of shifts in pupil positions in the gaze conditions (i.e. corresponding to 5° and 10° left or right, respectively). The results of this landmark experiment clearly revealed that adaptation to averted gaze had no influence on participants' line judgements and therefore produced a gaze-specific aftereffect, rather than a general spatial bias.

The second study on eye gaze adaptation also reported a series of three studies aiming at answering the same questions as Jenkins et al. (2006). The experimental design, however, differed from the study by Jenkins et al. (2006) in various aspects. First, Seyama and Nagayama (2006) used images of human faces which were generated by computer graphics software instead of real photographs. Second, they used adaptation stimuli that were characterised by a larger deviation from direct gaze (35°) whereas the test stimuli were characterised by smaller gaze deviations (2° and 4° left and right, respectively). Third, they had participants make two-alternative forced-choice decisions of whether a test face was gazing to the left or right and did not offer "direct gaze" as a response category. Despite these methodical differences, Seyama and Nagayama (2006) observed gaze adaptation aftereffects similar to those reported by Jenkins et al. (2006): after prolonged viewing of faces with eye gaze consistently directed to the left (or right) direction, participants most often perceived gaze directed directly at them as looking to the right (or left), respectively.

In addition to the basic experiment, the experiments excluding low-level adaptation or a general spatial bias were also very different from those of Jenkins et al. (2006). In order to rule out low-level adaptation effects, Seyama and Nagayama (2006) used displays of a pair of faces with opposite gaze directions as adaptation stimuli. The faces either showed neutral, happy, or surprised expressions, whereas the eye features in all faces were identical. In one adaptation condition, participants simultaneously observed leftward gaze in happy faces and rightward gaze in surprised faces ('happy/surprised condition'). In a second condition, the allocation of gaze directions to emotions was reversed ('surprised/happy condition'), and in a control condition both faces showed neutral expression. The authors found that happy faces elicited stronger aftereffects than surprised faces (i.e. participants adapted to the direction of eye gaze contained in the happy faces). This interaction of eye gaze direction and emotional expression suggests that gaze adaptation happened at a relatively high level of visual processing. Finally, rather than using a non-facial test stimulus to see if adaptation effects merely reflected general spatial mechanisms, Seyama and Nagayama (2006) used non-facial adaptation stimuli (arrows pointing to the left or right) and facial test stimuli in their third experiment. The results showed that adaptation to a right-pointing (or left-pointing) arrow did not have an influence on the estimations of gaze directions to the left or right direction.

Overall, the similarity of the results of the studies by Jenkins et al. (2006) and Seyama and Nagayama (2006) is remarkable, especially when considering the large differences in the stimulus sets, indicating that gaze direction aftereffects arise robustly over various conditions.

A study by Calder and colleagues (2007) has recently used eye gaze adaptation paradigms in order to gain further insight into the organisation of the brain structures involved in eye gaze perception. Using fMRI adaptation they investigated the functional organisation of the human STS region and showed that adaptation to one direction led to a decreasing BOLD response to test faces gazing into the adapted direction (relative to test stimuli showing eye gaze directed to the unadapted side or gazing directly at the observer). This decrease in BOLD activity was located in the anterior part of the STS. Resuming earlier fMRI studies and the results of their own study Calder et al. (2007) suggested that the anterior part of the STS selectively processes different gaze directions whereas the posterior STS region was proposed to be involved in perceiving the ‘intentionality’ revealed by eye gaze.

To summarise, several studies have demonstrated that our percept of the gaze direction in others can be severely altered as a consequence of adaptation. Above the pure demonstration of this, adaptation studies have made major contributions to the understanding of how eye gaze directions are neurally represented.

2.2.4 Gender Adaptation

The first study reporting aftereffects of adaptation to face gender was published by Webster, Kaping, Mizokami, and Duhamel (2004). They investigated the effects of adaptation to male or female faces on forced-choice gender decisions in response to images morphed along a male-female-continuum between the adaptor faces. Before and after adaptation, Webster et al. (2004) determined participants' individual category boundaries for that continuum, i.e. the morph levels at which both gender decisions were equally likely. Before adaptation, this boundary represented an androgynous image in an intermediate position between the female and male exemplars. After participants had adapted to male faces the category boundary was again determined and was found to be shifted towards the gender of the adapting stimulus, i.e. after adaptation to a male face, the previously ambiguous image appeared distinctly female. Analogous results were reported for adaptation to female faces. In order to rule out the explanation that observers only adapted to differences defining individual identity, Webster et al. (2004) repeated the experiment with a new set of adaptation stimuli. In this new experiment, identities of test stimuli were unrelated to the identities of adaptation stimuli. This manipulation did not have an influence on the gender adaptation effects: again, category boundaries were significantly shifted after adaptation, suggesting that the observed effects indeed reflected response changes of neural mechanisms underlying gender perception. Above that and consistent with other studies reporting an *own-gender bias* in sex discrimination, Webster et al. (2004) observed large individual differences in the category boundaries chosen during pre-adaptation trials. These differences were related to the categories to which the participants themselves belonged: female and male participants tended to choose gender boundaries in a male-female continuum that were shifted towards their own gender, indicating that observers may generally be more sensitive to how a face from their own category differs from others.

Following the rationale of a study investigating opposite adaptation effects for upright and inverted faces (Rhodes et al., 2004), Little, DeBruine, and Jones (2005) tested whether opposite effects of adaptation could be observed for male and female faces. In three experiments they had participants adapt to male and female faces that were realistically transformed in opposite directions with regard to their eye spacing, facial identity, or masculinity. They found gender-contingent face aftereffects in all three experiments. For example, adaptation to female faces with increased eye-spacing and to male faces with decreased eye-spacing induced simultaneous opposite aftereffects for male and female faces. Participants perceived female faces with increased eye-spacing as more normal than females with decreased eye-spacing whereas at the same time they perceived male faces with decreased eye-spacing as more normal than male faces with increased eye-spacing. These findings strongly suggest that distinct neural populations code subcategories of gender, namely male and female faces, as already proposed by Rhodes et al. (2003) and are not in line with the idea of one single face-space representing both male and female faces (Johnston, Kanazawa, Kato, & Oda, 1997).

Bestelmeyer et al. (2008) conducted a study further investigating gender-contingent aftereffects. They examined whether the differential aftereffects reported by Little et al. (2005) were really ‘category-contingent’, i.e. whether they were selective for the perceptual categories of male and female faces, or whether they were ‘structure-contingent’ and mainly reflected an adaptation of neurons coding structural aspects of faces which happen to be different for male and female faces. In order to answer this question, the authors examined whether opposite aftereffects could equally be observed for two groups of faces from distinct gender categories (i.e. male and female faces) and for two groups of faces of the same gender with structural differences that were physically identical to those between male and female categories (i.e. female and hyper-female). The authors found negative aftereffects only for the across-category but not for the within-category group and concluded that the gender-contingent aftereffects reported earlier could be attributed to adaptation of neurons coding perceptual gender category rather than high-level structural aspects in face configurations.

Kovács et al. (2006) investigated the neural correlates of face and hand gender adaptation processes. They had participants adapt to female faces, female hands, or control stimuli. The behavioural results revealed clear negative aftereffects of adaptation to female faces as compared to control adaptation stimuli replicating earlier studies. Interestingly, negative aftereffects of gender adaptation could also be observed for female hands. However, these aftereffects appeared to be category-specific as there were no aftereffects when the adaptor and test stimulus belonged to different categories: gender adaptation did not occur when a hand served as the adaptation stimulus and a face was used as test stimulus or vice versa. The analysis of ERPs in response to test stimuli revealed that adaptation to both hands and faces resulted in a strong and category-specific modulation of the N170 with reduced amplitudes and increased latencies following adaptation to hands or faces as compared to the control condition in which participants adapted to Fourier randomised versions of the adaptors. Kovács et al. (2006) therefore suggested that the modulation of the N170 component induced by face adaptation might be regarded as the primary correlate of shape-selective visual adaptation in humans.

Kovács, Zimmer, Harza, Antal, and Vidnyanszky (2005) investigated the effects of adaptation to female stimuli presented in only one visual hemifield on the perception of gender-ambiguous test stimuli presented in the same (overlapping condition) or a different hemifield (non-overlapping condition). The authors showed that adaptation resulted in a strong perceptual aftereffect in both cases, i.e. in both the overlapping and non-overlapping condition test faces were perceived more masculine than in the pre-adaptation phase. However, adaptation effects were not completely independent of the locations of adaptation and test stimulus: the magnitude of the aftereffect was significantly larger when the adaptor and test faces were spatially overlapping than when they were not overlapping. The ERPs recorded in this experiment also revealed that adaptation to a female face stimulus as compared to a control stimulus (a Fourier image) had a significant effect on the amplitude of the N170 component evoked by the test stimulus (cf. Kovács et al., 2006). Kovács et al. (2005) found that the N170 amplitudes in the non-adapted condition were significantly larger than N170 amplitudes in both the overlapping and non-overlapping adaptation conditions.

When analysing N170 amplitudes separately for the two hemispheres, they found that the adaptation effects over the left hemisphere were significantly larger in the overlapping than in the non-overlapping conditions. For the right hemisphere, however, no such position-specific differences were found. Finally, separate analyses were conducted on the N170 amplitudes evoked by ipsilaterally and contralaterally presented test stimuli. For contralateral test stimuli, they revealed that N170 adaptation effects over both hemispheres were significantly larger in the overlapping than in the non-overlapping condition. For ipsilateral test stimuli, however, N170 adaptation effects were significantly larger in the non-overlapping than in the overlapping condition over the right, but not over the left hemisphere.

Overall, the authors concluded that effects of gender adaptation consist of a position invariant and non-invariant component (see also Zhao & Chubb, 2001 for similar effects concerning size invariance of the face distortion aftereffect). Concerning their finding of major differences in N170 adaptation effects between spatially overlapping and non-overlapping adaptor and test stimuli over the hemisphere contralateral to the test stimulus, Kovács et al. (2005) suggested that their behavioural adaptation effects primarily resulted from the adaptation of shape-selective neural processes in the hemisphere contralateral to the test stimulus.

This result may be seen in some contradiction to earlier studies which reported other high-level face aftereffects to be independent of retinotopic mapping (Leopold et al., 2001; Jenkins et al., 2006). These studies, however, investigated identity or gaze direction aftereffects, whereas the study by Kovács et al. (2005) investigated gender aftereffects. The different findings might therefore, at least in part, be explained by the assumption that different facial aspects (e.g. identity, gaze direction, or gender) are processed by distinct neural entities (Haxby et al., 2000) that might be characterised by differences in their adaptation mechanisms.

In a later study Kovács, Zimmer, Harza, and Vidnyanszky (2007) investigated whether adaptation duration had differential effects on position-specific and position-invariant components of face gender aftereffects. In line with their earlier study (Kovács et al., 2005), they found facial aftereffects evoked by long-term adaptation (5 s) to be characterised by both a position-invariant and a position-specific component. Short-term adaptation (500 ms), however, led to negative aftereffects that were entirely position-invariant. Consistent with these behavioural findings, only the adaptation effects on N170 amplitudes obtained after long-term adaptation were found to consist of a position-specific component – following short-term adaptation this was not the case. To sum up, the authors concluded that the timing of adaptation might be a critical factor in determining which cortical areas react to the adaptation procedure (see also Fang, Murray, & He, 2007).

As mentioned before, other kinds of social stimuli apart from facial information also support gender perception: Concerning voice perception, Schweinberger et al. (2008; see also Mullennix, Johnson, Topcu-Durgun, & Farnsworth, 1995) have recently reported negative perceptual aftereffects following adaptation to gender in voices. In a series of experiments they showed that adaptation to unfamiliar male voices causes subsequently presented voices to be perceived as more female (and vice versa). In line with the findings of Kovács et al. (2006) adaptation effects did not occur across stimulus categories: Adaptation to female or male names or to silent videos of articulating female or male faces did not produce any aftereffects on the perception of subsequently presented voices.

Similarly, the perception of biological motion which has also been proved a reliable source for gender discrimination (Barclay et al., 1978; Kozlowski & Cutting,

1977) has been shown to be biased by adaptation. Adaptation to the gait pattern of one gender biased participants to judge subsequent gait patterns as representing the opposite gender (Jordan et al., 2006). After viewing a male point light walker (PLW) participants were more likely to judge a subsequently presented ambiguous PLW as female, and vice versa.

2.2.5 Summary and aim of the present studies

To summarise, adaptation studies on basic physical stimulus characteristics have a very long tradition and have provided important insight into the coding mechanisms of different stimulus attributes, such as motion. The more recent finding of similar aftereffects in high-level vision evoked by complex visual stimuli such as faces has already been proved to be of equal value for perception research. To name only a few aspects, selective adaptation effects have been found for facial identity, facial gender, and eye gaze direction. Respectively, these studies revealed insight into the nature of representation of facial identities in terms of deviance from a prototypical face, the selective coding of male and female faces, and provided evidence that gaze direction is not only coded in terms of direct vs. averted gaze but that distinct cell populations selectively process left and right gaze.

Research combining adaptation paradigms with modern electrophysiological and neuroimaging methods is only at its beginning; however, first studies have already been published and revealed promising new approaches to understanding the processing of complex visual stimuli. Although the investigation of shape-specific high-level adaptation effects is only a relatively recent development, there are already a number of studies investigating adaptation in fMRI whereas the electrophysiological correlates of high-level adaptation have so far hardly been examined. Whereas first studies on the neural correlates of gender adaptation proved that the application of both methods can be successfully combined (Kovács et al., 2006), the investigation of ERP correlates of other adaptation effects has so far been neglected. This is especially surprising as electrophysiological studies have a long tradition in face perception research which has led to the possibility of comparing new adaptation-related findings to well-established effects.

The studies described in this thesis were designed in order to close that gap. Studies 1 and 2 investigated the electrophysiological correlates of the eye gaze adaptation effect. Study 3 aimed at a further investigation of the nature of high-level adaptation effects in describing temporal aspects of gaze adaptation. Whereas the temporal aspects of low-level adaptation have been thoroughly examined, a close monitoring of the duration of high-level aftereffects and the time course of their decline has not yet been performed. Aiming at a further comparison of the characteristics of low-level and high-level adaptation effects, Study 3 therefore investigated gaze adaptation effects with a paradigm modified to capture long-term effects of adaptation.

Finally, Study 4 investigated the neural correlates of adaptation to both face and voice gender on the perception of faces and aimed at a deeper understanding of the modality-specificity of gender adaptation effects. The study also further tested a methodological modification of the ERP adaptation paradigm which had first been applied in Study 2. This new experimental condition aimed at disentangling the relative influences of general face adaptation and adaptation to specific facial characteristics (i.e. eye gaze direction and the gender of a face, respectively).The application of this modification in Study 4 therefore allowed to judge the general benefit of the methodological improvement outside the field of gaze perception.

3. Experiment 1: Neural correlates of gaze adaptation I

3.1 Introduction

As has been described in greater detail in the main introduction (see chapter 2.1.2) the efficient perception of other people’s gaze direction has been shown to be of special importance for social interactions. Eye gaze is a key signal for exercising social control, it is used to estimate the focus of spatial attention in others, and is able to trigger fast ‘reflexive’ attentional shifts in observers (e.g. Friesen & Kingstone, 1998; Schuller & Rossion, 2001). There is evidence from neurophysiological research suggesting that gaze signals may be processed by a specific neuronal circuitry involving areas in the superior temporal sulcus, in which cells selectively responding to different directions of gaze have been identified in macaques (Perrett et al., 1992). Functional imaging studies propose that regions within the same structures are also involved in gaze perception in humans (Hoffman & Haxby, 2000). A posterior region within human superior temporal sulcus might be sensitive to observing eye *movements* in others (Puce & Perrett, 2003).

The investigation of ERP correlates of gaze perception provided some evidence that the perception of the eye region is mainly reflected in the occipitotemporal N170 component. Several studies reported the N170 amplitude and latency evoked by isolated eye stimuli as being enhanced as compared to the presentation of full faces (Bentin et al., 1996; Itier et al., 2006; Itier, Alain, Sedore, & McIntosh, 2007b; Jemel et al., 1999) and it has even been suggested that the N170 face inversion effect is mainly due to the inversion of the eye region (Doi et al., 2007; Itier et al., 2006; Itier et al., 2007b). Faces with closed eyes were found to evoke a significantly delayed N170 as compared to both averted and direct gaze (Taylor et al., 2001). Studies directly assessing the processing of gaze direction found larger N170 amplitudes in response to eye aversion than in response to direct eye gaze (Itier et al., 2007a; Puce et al., 2000; Watanabe et al., 2002; but see Conty, N'Diaye, Tijus, & George, 2007, for a study reporting opposite results). Together, these findings accumulated support for the hypothesis that the N170 might reflect the activity of an eye detector (Bentin et al., 1996; see also Itier et al., 2006) but it remains unclear how precisely the perception of gaze direction and gaze movements in others is coded in brain activity.

Recently, a powerful adaptation effect was demonstrated for the perception of eye gaze: Adaptation to lateral gaze (25°) virtually eliminated observers’ perception of smaller gaze deviations (5° and 10°) in the adapted direction; gaze to that side was erroneously perceived as gazing directly at the observer (Jenkins et al., 2006). The finding of very similar results in another study (Seyama & Nagayama, 2006) using different stimulus materials and experimental parameters suggests that gaze direction aftereffects can reliably be observed under various conditions (see chapter 2.2.3, for a detailed comparison of the two studies).

Experiment 1 aimed at extending these novel gaze adaptation effects by introducing a short time interval between adaptation and test stimuli both to ensure a clean ERP baseline and to test whether gaze adaptation effects will survive the short interval, and by investigating the neural correlates of adaptation using event-related potentials. The focus was primarily on the face-elicited N170 due to the strong evidence that this component is driven by the eye region and is thought to be at least partially generated by the posterior superior temporal sulcus region in tasks that involve the perception of eye movements in others (Puce et al., 2000).

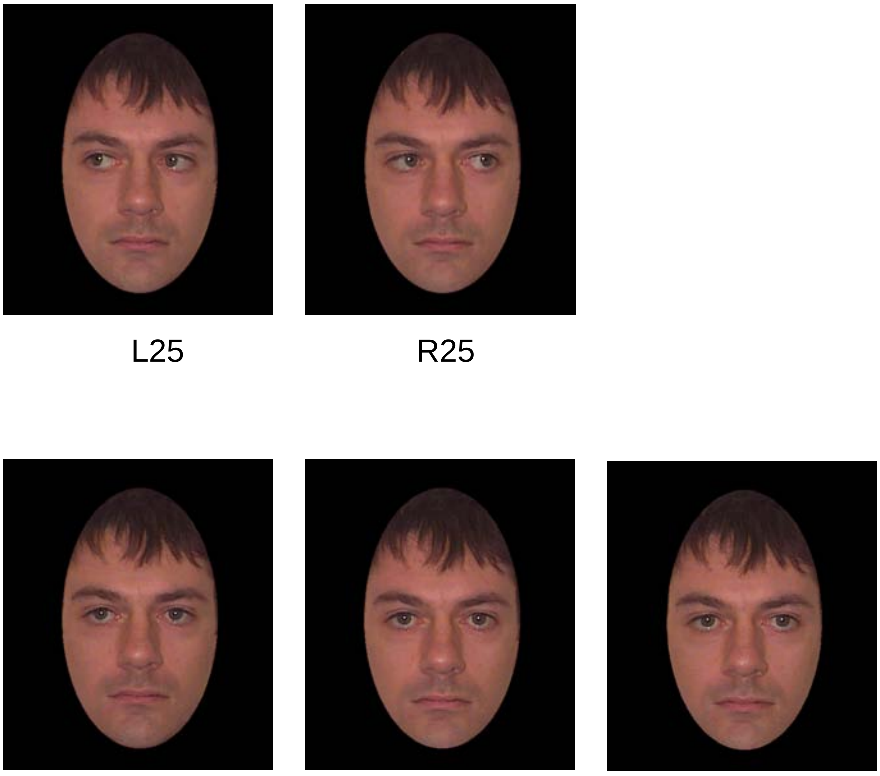
3.2 Methods

Participants

Ten naïve participants (19 to 26 years, *M* = 22.3 years, 3 men) contributed data and received course credit or payment for their participation. They all reported normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Participants gave their informed consent prior to the data acquisition.

Stimuli

Test faces were colour photographs of 6 male and 6 female young adults used in a previous study (Jenkins et al., 2006). Each model posed at three different angles of gaze: 5° left (L05), direct (S00), and 5° right (R05; all directions from the observer's point of view). Photos of the same 12 models gazing 25° to the left (L25) or right (R25) were also available, and were used as adaptation stimuli (for an example of the stimuli, please see Figure 7). Test faces (10.3 x 17.5 cm) were presented at a viewing distance of ~87 cm which was kept constant by using a chin rest. In order to exclude the possibility that the observed effects mainly reflect effects of low-level adaptation, adaptation stimuli were presented at 90% the size of the other stimuli so that the eye regions in adaptation and test stimuli were non-overlapping.



L25 R25

L05 S00 R05

Figure 7: Example of gaze directions used in Experiment 1. Upper row: Faces with gaze deviations of 25° left and 25° right were used as left and right adaptors, respectively. Lower row: Stimuli gazing 5° left, directly at the observer, or 5° right served as test stimuli.

Apparatus

ERPs were recorded on 32 Ag/AgCl electrodes (AC, 0.05 – 40 Hz, 250 Hz sampling rate) at the positions Fz, Cz, Pz, Iz, Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10, PO9, and PO10, with TP10 as initial common reference, using an Easy-Cap^{TM}. Electrode impedances were kept below 10 kΩ. The horizontal electrooculogram (EOG) was recorded from the outer canthi of both eyes, and the vertical EOG was monitored bipolarly from above and below the right eye. Data were segmented into epochs of 2200 ms (200 ms prestimulus baseline). Offline, trials were visually inspected for ocular (e.g. blinks, saccades) and non-ocular artifacts. Trials with non-ocular artifacts and saccades were discarded. For all other trials, ocular blink contributions to the EEG were corrected in KN using a regression method (Elbert, Lutzenberger, Rockstroh, & Birbaumer, 1985). ERPs were digitally low-pass filtered at 10 Hz (zero phase shift, 12 dB/oct), and recalculated to average reference.

Task and Procedure

The experiment began with a *pre-adaptation test* to determine the baseline ability to identify gaze direction. Using right index, middle, and ring fingers on three response keys, participants indicated if a test face showed left, direct, or right gaze direction. All 36 test faces (12 identities x 3 gaze directions) were repeated 3 times in random order. For each trial, a question mark was first presented (800 ms), was then replaced by the test face (400 ms), followed by a blank screen for 2250 ms during which participants responded.

Two *adaptation blocks* (left or right adaptation, block order counterbalanced across participants) followed the pre-adaptation test. In each block, twelve adaptation stimuli with gaze averted 25° in one constant direction were presented twice in randomised order. Exposure duration was 3500 ms each with an inter-stimulus interval of 200 ms. Each adaptation sequence was immediately followed by a *post-adaptation test*. This was the same as the pre-adaptation test, except that each test stimulus was preceded by two consecutive top-up adaptation displays (3500 ms each). In order to exclude potential effects of immediate repetition priming (Schweinberger et al., 2004) neither of the two top-up adaptation stimuli carried the same identity as the following test face. To address the issue of whether adaptation would survive a short time interval, and to ensure a clean ERP baseline interval, a 1000 ms interval separated the offset of the second top-up adaptation display and the onset of the test display.

3.3 Results

3.3.1 Behavioural Results

In the pre-adaptation test, participants were highly accurate at discerning direct gaze (*M* = 90.8 ± 8.6%), and fairly accurately classified left (*M* = 70.3 ± 15.6%) and right gaze (*M* = 71.0 ± 19.2%). After adaptation to gaze averted 25° in one direction, however, perception of gaze directed to that side was nearly eliminated (*M* = 3.4% and *M* = 8.1% for left and right gaze, respectively), and gaze in the adapted direction was perceived as looking directly at the observer in ~90% of the trials (see Figure 8). An analysis of variance (ANOVA) on percentages of “direct” responses, with the factors Adaptation (left, right, pre-adaptation) and Test stimulus (left, right, direct) revealed an interaction of Adaptation and Test stimulus, (*F*[4, 36] = 151.5, *p* < .001).

This was due to a strong increase of “direct” responses to left gazing test faces after left adaptation as compared to the pre-adaptation test (*t*[9] = 10.3, *p* < .001), and a strong increase of “direct” responses to right gazing test faces after right adaptation as compared to the pre-adaptation test (*t*[9] = 8.5, *p* < .001).

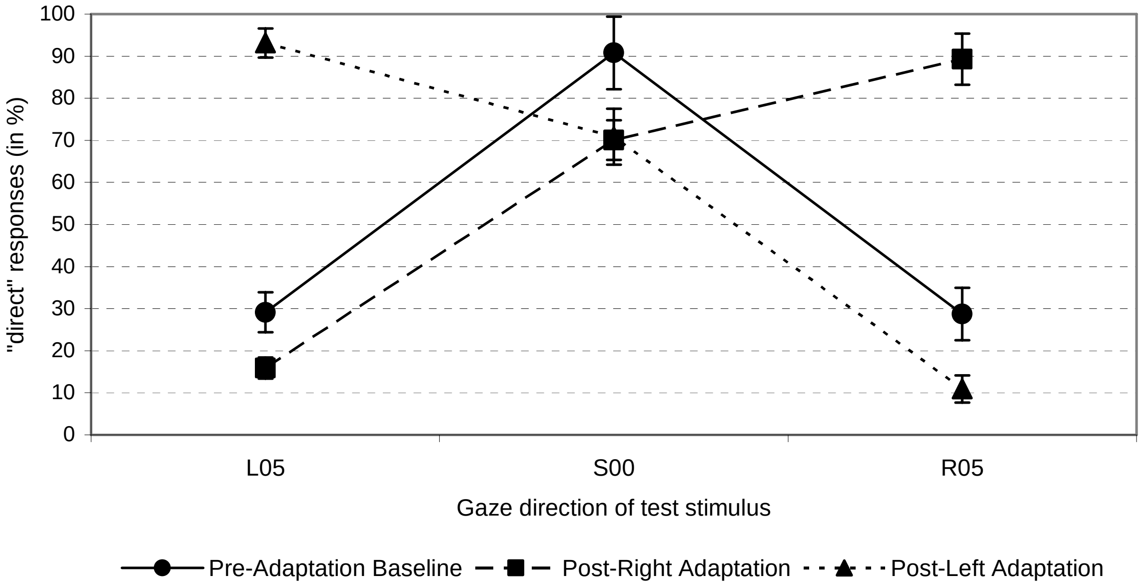


Figure 8: Percentages of “direct” responses (mean across 10 observers) for the three different gaze angles of test faces. Responses are displayed, depending on whether test faces were shown before adaptation (solid lines) or after adaptation to either left (dotted lines) or right (dashed lines) eye gaze.

3.3.2 Electrophysiological Results

For ERPs to test faces, mean amplitudes in the time segment 90-130 ms (P100) were calculated at 8 occipitotemporal electrodes (O1, O2, TP9, TP10, P9, P10, PO9, and PO10). Mean amplitudes for time segments 150-200 ms (N170) and 250-350 ms were taken at 8 posterior electrodes (P7, P8, TP9, TP10, P9, P10, PO9, and PO10). Peak latencies of P100 and N170 were determined at PO10 (80-150 ms and 130-220 ms windows).

P1

Analogous ANOVAs as for behavioural data were run with the additional factors Electrode site and Hemisphere. There was a significant effect of adaptation on the P100 (*F*[2, 18] = 6.7, *p* < .01, see Figure 9). While the P100 amplitude was significantly more positive after both left- and right-adaptation relative to the pre-adaptation test (*p* < .01), P100 amplitude was equivalent after left- and right-adaptation blocks (*p* > .20).

Effects of adaptation on P100 latency (*F*[2, 18] = 51.3, *p* < .001) reflected shorter latencies for pre-adaptation blocks (*M* = 122.4 ± 6.8, 123.7 ± 8.5, and 111.3 ± 7.3 ms for left-, right-, and pre-adaptation, respectively). No further effects or interactions were found (all *p*s > .20), and there were no differences between left- and right-adaptation blocks (*p* > .20).

N170

Similar to the results obtained for the P1 time window, there was an effect of adaptation on N170 amplitude, both as a main effect (*F*[2, 18] = 4.5, *p* < .05) and in interaction with Site (*F*[6, 54] = 15.5, *p* < .001), however, this was entirely due to the fact that N170 amplitude was significantly smaller following both left- and right-adaptation relative to the pre-adaptation test (see Figure 9). N170 was equivalent for left- and right-adaptation blocks (*p* > .20).

Effects of adaptation on N170 latency were also significant (*F*[2, 18] = 17.3, *p* < .001), again with shorter latencies for pre-adaptation blocks (*M* = 186.9 ± 17.3, 189.3 ± 19.1, and 170.4 ± 13.5 ms for left-, right-, and pre-adaptation blocks, respectively). No further effects or interactions were found (all *p*s > .20), and there were no latency differences between left- and right-adaptation blocks (*p* > .20).

250–350 ms

The 250-350 ms segment was the only time segment that revealed ERP differences between left- and right-adaptation blocks (*F*[3, 27] = 3.5, *p* < .05) for the interaction Adaptation x Site, due to a right posterior positivity following left- vs. right-adaptation (see Figures 9 and 10). Note that this effect was similar across the test stimuli, and there was no interaction involving test stimulus (*p* > .20).

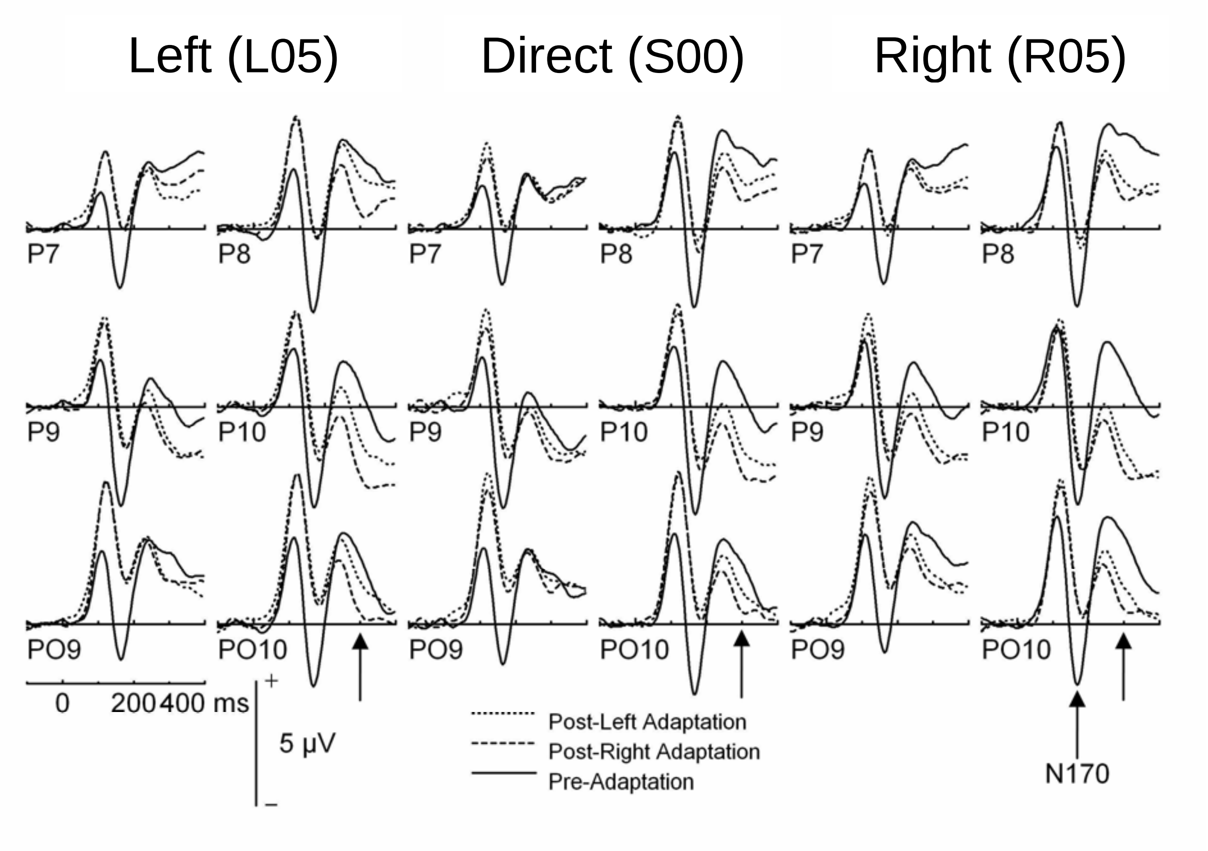


Figure 9: Grand average ERPs across 10 observers, for the three different gaze angles of test faces depending on whether these faces were shown before adaptation (pre-adaptation baseline, solid lines) or after adaptation to either left (dotted lines) or right (dashed lines) eye gaze. Recordings are shown for a selected set of posterior electrodes. Arrows indicate the N170 and the larger right positivity ~250 – 350 ms after adaptation to left vs. right gaze.

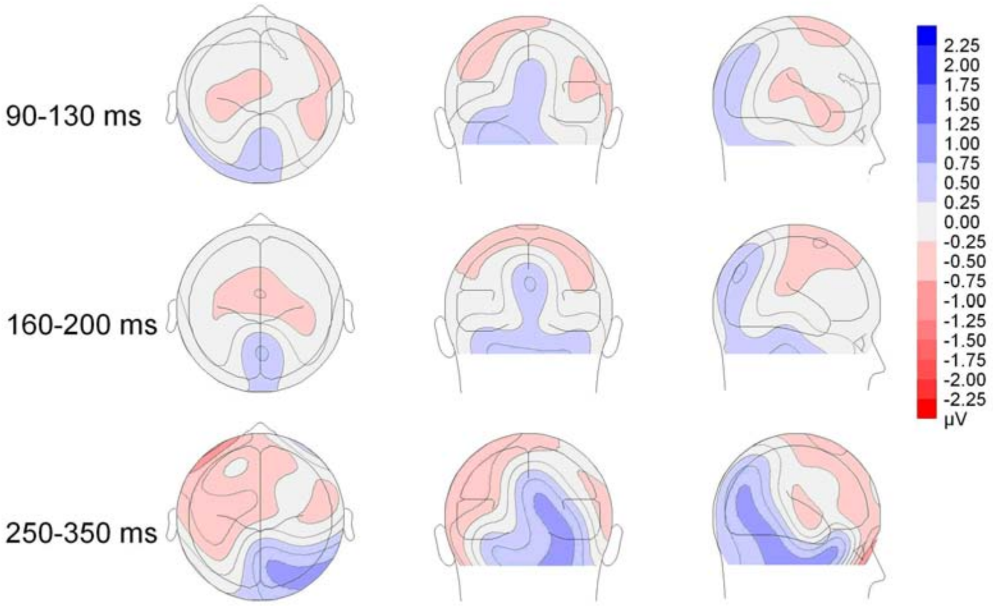


Figure 10: Voltage maps (spherical spline interpolation, 110º equidistant projection) for the ERP difference (left-minus right-adaptation) averaged across test stimulus. Note the right posterior positivity (in blue) ~250-350 ms and the absence of direction-specific adaptation effects in the preceding P100 and N170 time segments.

3.4 Discussion

The study demonstrated a striking adaptation effect to lateral eye gaze: the ability to perceive small gaze deviations was virtually eliminated after adaptation to gaze strongly diverted to the same direction. Intriguingly, the present adaptation effect was of similar size as the effect reported by Jenkins et al. (2006), despite the fact that a 1 s interval had been introduced between adaptation and test stimulus, indicating that gaze adaptation effects survive a short time interval. However, the precise time course of gaze adaptation is as yet unclear, and researchers have only begun to study the time course of adaptation for other facial aspects (Leopold, Rhodes, Muller, & Jeffery, 2005).

In spite of striking effects of gaze adaptation on the perception of test stimuli, and although the N170 has been linked to the perception of eyes (Itier et al., 2006; Itier et al., 2007b; Schyns, Jentzsch, Johnson, Schweinberger, & Gosselin, 2003), N170 was completely unaffected by the direction of prior gaze adaptation. To the extent that the present N170 in gaze perception is generated by posterior superior temporal sulcus regions (Puce et al., 2000), this suggests that gaze adaptation does not modify processing ~170 ms in those regions. It is, however, important to note that despite the prominent role of the eye region for the N170, the sensitivity of N170 for gaze direction is also controversial; with some studies reporting larger N170 amplitudes in response to averted eye gaze (Itier et al., 2007a; Puce et al., 2000; Watanabe et al., 2002), others reporting larger amplitudes in response to direct gaze (Conty et al., 2007), and yet others reporting no difference in N170 amplitudes to direct and averted gaze at all (Taylor et al., 2001).

While there were no direction-specific effects of gaze adaptation on N170, smaller and later N170 responses were elicited by the same test faces during the post-adaptation blocks than during the pre-adaptation block. This unexpected finding may be tentatively ascribed to the fact that test faces were shown more than 3000 ms after a previous test face in the pre-adaptation block, but only 1000 ms after a previous top-up adaptor face in post-adaptation blocks. The reduced and delayed N170 in post-adaptation blocks might thus reflect adaptation of a mechanism that is sensitive to the detection of face-like stimuli (irrespective of specific information such as gaze, gender, or identity) and that is reflected in the N170 (Schweinberger et al., 2004). While this interpretation can be reconciled with previous results on adaptation for other types of facial information (Kovács et al., 2006), this issue clearly deserves further investigation. One implication for studies using ERPs (N170) to investigate facial adaptation is that these should use adaptation conditions which differ with respect to the adaptation-relevant information only (e.g., for gaze adaptation: left vs. direct vs. right gaze adaptors, for gender adaptation: male vs. androgynous vs. female adaptors), while faces are used as adaptors throughout.

Despite the absence of direction-specific gaze adaptation effects on N170 there was a later adaptation effect ~250-350 ms over right posterior regions (which surprisingly did not interact with the gaze direction of the test stimulus). This may be an interesting parallel to a recent fMRI study of gaze adaptation, which also reported no adaptation effects on posterior superior temporal sulcus regions, whereas adaptation effects were found in more anterior superior temporal sulcus regions as well as the inferior parietal cortex (Calder et al., 2007). Overall, the present findings suggest that adaptation does not modify gaze processing ~170 ms in posterior superior temporal sulcus regions, but alters subsequent processes that may be mediated by more anterior temporal areas of the right hemisphere.

4. Experiment 2: Neural correlates of gaze adaptation II

4.1 Introduction

While the results of Experiment 1 did not provide evidence for a gaze direction-specific modulation of the N170, they clearly showed some impact of the general adaptation procedure on this component. Following adaptation to either gaze direction, the N170 was characterised by reduced amplitudes and increased latencies as compared to pre-adaptation trials. Modulations specific for the gaze directions of the adaptation stimuli were measured not earlier than ~250 – 350 ms with larger right posterior positivity following adaptation to left than right direction. Surprisingly, this effect was found to be unaffected by the gaze direction of the test stimuli. Experiment 2 was designed to further examine the nature of gaze adaptation and to answer the major question concerning the nature of the N170 effect observed in Experiment 1.

A possible way to account for the effects observed in the N170 time range is the assumption that they reflect adaptation to more general face-related information, such as the structural composition of faces per se. This is in line with the general idea of the N170 as predominantly reflecting the processing of structural (or configural) face information in upright face stimuli (Bentin et al., 1996; Kanwisher & Moscovitch, 2000; Rossion et al., 2000). To examine this hypothesis the adaptation procedure of Experiment 2 was modified in a way that allows for a comparison of the effects of adaptation to a certain gaze direction (i.e. adaptation to right gaze) and to a direction-neutral adaptation condition (i.e. adaptation to direct gaze) which replaced the control (pre-adaptation) condition of Experiment 1. This modification solves the major methodical concern related to Experiment 1, namely the different quantity of general face information that preceded test stimuli in the pre- and post-adaptation phases. More precisely, the control condition applied in Experiment 2 contains a series of ‘adaptation’ faces and top-up stimuli presented before each test face. These adaptation and top-up stimuli, however, do not contain directional eye gaze information but they consist of faces gazing directly at the observer.

Another major change compared to Experiment 1 is related to the choice of adaptation stimuli. Considering the fast neural recovery of adaptation (which is the major basis of fMRI adaptation paradigms), it might be possible that the relatively small influence of adaptation found on the ERPs to test faces in Experiment 1 was due to the large perceptual difference between adaptation and test stimuli used. Participants adapted to faces showing strongly averted eye gaze (25°), they were, however, tested with faces showing only slightly averted eye gaze (5°). Therefore, it has to be considered that the presentation of only marginally deviating eye gaze in the test condition may generally have led to nearly complete recovery from adaptation of neurons responding to eye gaze that largely deviates from direct gaze. This recovery process might have covered the activity of neurons responsible for the behaviourally found adaptation effects. More precisely, it is possible that the adaptation procedure affected the response characteristics of a larger number of neurons than those responsible for the behaviourally found adaptation effect and that the recovery of adaptation in this additional number of neurons might have made it difficult to detect the relatively small change in response properties of the neurons that still showed some residual influence of the adaptation procedure. To account for this potential drawback, the effects of adaptation to stimuli with relatively small gaze deviations (10°) on the perception of test stimuli with smaller or identical gaze angles (5° and 10°) have been investigated in Experiment 2.

Finally, in order to more directly monitor the process of adaptation itself, Experiment 2 also directly examined ERPs in response to the adaptation stimuli. This allowed for a characterisation of the immediate effects of adaptation without possible influences of recovery processes.

4.2 Methods

Participants

Twenty naïve participants (20 to 28 years, *M* = 22.7 years, 10 men) which were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) contributed data and received course credit or payment for their participation. They all reported normal or corrected-to-normal vision and gave their informed consent prior to data acquisition.

Stimuli

Test faces were colour photographs of the same 6 male and 6 female young adults as used in Experiment 1 and a previous study (Jenkins et al., 2006). Each model posed at five gaze angles: 10° left (L10), 5° left (L05), direct (S00), 5° right (R05), and 10° right (R10; all directions from the observer's point of view). A subset of these stimuli also served as adaptation stimuli: The stimuli showing direct gaze

(S00) served as control (direct) adaptors and the stimuli showing 10° gaze deviation to the right (R10) served as right adaptors.

Test faces (8.0 x 14.0 cm) were presented at a viewing distance of ~87 cm which was kept constant by using a chin rest. Adaptation stimuli were presented at 150% the size of test stimuli so that the eye regions in adaptation and test stimuli were non-overlapping.

Apparatus

The EEG was recorded from 32 Ag/AgCl electrodes (AC, 0.05 – 40 Hz, 250 Hz sampling rate) at locations Fz, Cz, Pz, Iz, Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10, PO9, and PO10, with TP10 as initial common reference, using an Easy-Cap^{TM}. Electrode impedances were kept below 10 kΩ. The horizontal electrooculogram (EOG) was recorded from the outer canthi of both eyes, and the vertical EOG was monitored bipolarly from above and below the right eye. Offline, data were segmented into epochs of 2200 ms (200 ms prestimulus baseline) and trials were inspected for ocular (e.g. blinks, saccades) and non-ocular artifacts. Trials with non-ocular artifacts were discarded. For all other trials, the EEG was corrected for contributions of vertical and horizontal eye movements using BESAs automatic EOG artifact correction which is based on an adaptive artifact correction (Ille, Berg, & Scherg, 2002). Data were digitally low-pass filtered at 20 Hz (zero phase shift, 12 dB/oct), and recalculated to average reference.

Task and Procedure

The experiment began with a *pre-adaptation test* (identical to the one in Experiment 1) which was announced as a block of practice trials. The results allowed determining participants' baseline ability to identify eye gaze direction without any prior adaptation. Using right index, middle, and ring fingers on three response keys, participants indicated whether a test face showed left, direct, or right gaze direction. Altogether, 'practice trials' consisted of 72 test faces, with each of the twelve identities presented once in each of the L10, L05, R05, and L10 conditions and twice in the S00 condition. For each trial, a question mark was first presented (800 ms), was then replaced by the test face (400 ms), followed by a blank screen (2250 ms) during which participants responded. The implementation of this *pre-adaptation test* aimed at comparing its results to the behavioural data recorded in the new control condition – the direct gaze adaptation condition – therefore allowing the examination of possible effects of adaptation to direct gaze. During this stage of the experiment no EEG was recorded.

The major experiment consisted of two main blocks: One half of the experiment investigated the effect of adaptation to direct eye gaze, the other half examined the effect of adaptation to right eye gaze direction – with block order counterbalanced across participants. At the beginning of each block, twelve adaptation stimuli with gaze constantly directed in the direction of adaptation were presented twice in randomised order. Exposure duration was 3500 ms each with an inter-stimulus interval of 200 ms. This sequence was immediately followed by a *post-adaptation test* with 216 test trials. These test trials consisted of 36 presentations (12 identities x 3 repetitions) of L10, L05, R05, and R10 stimuli respectively and of 72 presentations (12 identities x 6 repetitions) of S00 stimuli. The presentation of an equal number of test stimuli gazing in the left direction (L10, L05), right direction (R10, R05), and directly at the observer (S00) aimed at requiring an equal amount of “left”, “right”, and “direct” responses therefore preventing participants from a response bias. Post-adaptation trials began with the presentation of a top-up adaptation display (3500 ms) which did not carry the same identity as the subsequently presented test face, followed by the presentation of a question mark (1000 ms), the test stimulus (400 ms), and a blank screen during which participants responded (2300 ms). To maintain a high level of adaptation throughout the *post-adaptation test* the blocked presentation of adaptation stimuli was repeated after 108 trials. After each series of 54 *post-adaptation test* trials the experiment was interrupted for a self-paced break.

4.3 Results

4.3.1 Behavioural Results

First, the patterns of “direct” classifications obtained in the pre-adaptation test (no adaptation condition) and in the control condition (direct adaptation condition) were analysed (see Table 1 and Figure 11). A repeated measurements ANOVA with the factors Adaptation (no, direct) and Direction of gaze in test faces (L10, L05, S00, R05, and R10) revealed no main effect of adaptation ($F[1, 19] < 1$) and no significant interaction with this factor ($F[4, 76] < 1$). This finding indicates that adaptation to direct gaze did not lead to aftereffects, and that the direct gaze adaptation condition can therefore serve as a neutral control condition for the main experiment.

	left gaze direction		direct gaze	right gaze direction	
	10° deviance	5° deviance		5° deviance	10° deviance
Pre-Adaptation Baseline	2.50 (1.06)	29.17 (3.05)	85.62 (2.45)	36.25 (4.33)	3.33 (1.27)
Post-Direct Adaptation	1.81 (0.61)	28.33 (2.93)	89.65 (1.64)	33.47 (5.45)	5.97 (2.43)
Post-Right Adaptation	1.39 (0.68)	20.00 (3.02)	84.58 (2.63)	64.17 (5.18)	13.33 (3.65)

Table 1: Mean percentages of “direct” classifications in response to test stimuli with left (5°, 10°), direct, and right (5°, 10°) gaze direction as obtained in the pre-adaptation baseline, the post-direct adaptation, and the post-right adaptation conditions (see also Figure 11).

In a second step, the behavioural results of the main experiment were analysed in a repeated measurements ANOVA. As participants were presented with an equal amount of test stimuli gazing to the left, right, and directly at the observer but only test stimuli gazing to the left or right were further characterised by a different degree of deviance from direct gaze (5°, 10°), behavioural data were analysed in two steps. In the first step, a repeated measurements ANOVA was conducted to analyse the effects of adaptation on the perception of test stimuli gazing in the left or right direction – including an analysis of the effect of deviance. This ANOVA with the factors Adaptation (direct, right), Deviance (5°, 10°), and Direction (left, right) revealed significant main effects of adaptation ($F[1, 19] = 17.50$, $p < .01$), deviance ($F[1, 19] = 172.09$, $p < .001$), and direction ($F[1, 19] = 23.14$, $p < .001$). Further, there were significant two-way interactions between the factors Adaptation and Deviance ($F[1, 19] = 6.19$, $p < .05$), Adaptation and Direction ($F[1, 19] = 97.32$, $p < .001$), Deviance and Direction ($F[1, 19] = 30.99$, $p < .001$), and a significant interaction between all three factors ($F[1, 19] = 54.17$, $p < .001$).

In order to further examine this three-way interaction, separate ANOVAs were conducted for left and right gazing test stimuli with Adaptation and Deviance as factors. The analyses of responses to test stimuli of both test directions revealed significant main effects of adaptation ($F[1, 19] = 5.84$, $p < .05$ and $F[1, 19] = 63.89$, $p < .001$, for analyses of responses to test stimuli with left and right gaze direction, respectively), main effects of deviance ($F[1, 19] = 104.55$, $p < .001$ and $F[1, 19] = 144.10$, $p < .001$), and significant interactions between the factors ($F[1, 19] = 5.82$; $p < .05$ and $F[1, 19]= 31.22$; $p < .001$). Further analyses of the interactions revealed that test stimuli with right gaze direction received significantly more incorrect “direct” classifications when presented following adaptation to right direction as compared to direct gaze adaptation – the difference was significant for both test stimuli deviating 5° (*t*[19] = 7.72, *p* <. 001) and 10° from direct gaze (*t*[19] = 3.58, *p* < .01, for means see Table 1). For test stimuli with left gaze direction this pattern was reversed and there were significantly more incorrect "direct" classifications following adaptation to direct gaze as compared to right gaze adaptation, but only for test stimuli deviating 5° from direct gaze (*t*[19] = 2.47, *p* < .05) and not for test stimuli deviating 10° from direct gaze (*p* > .5, for means see Table 1).

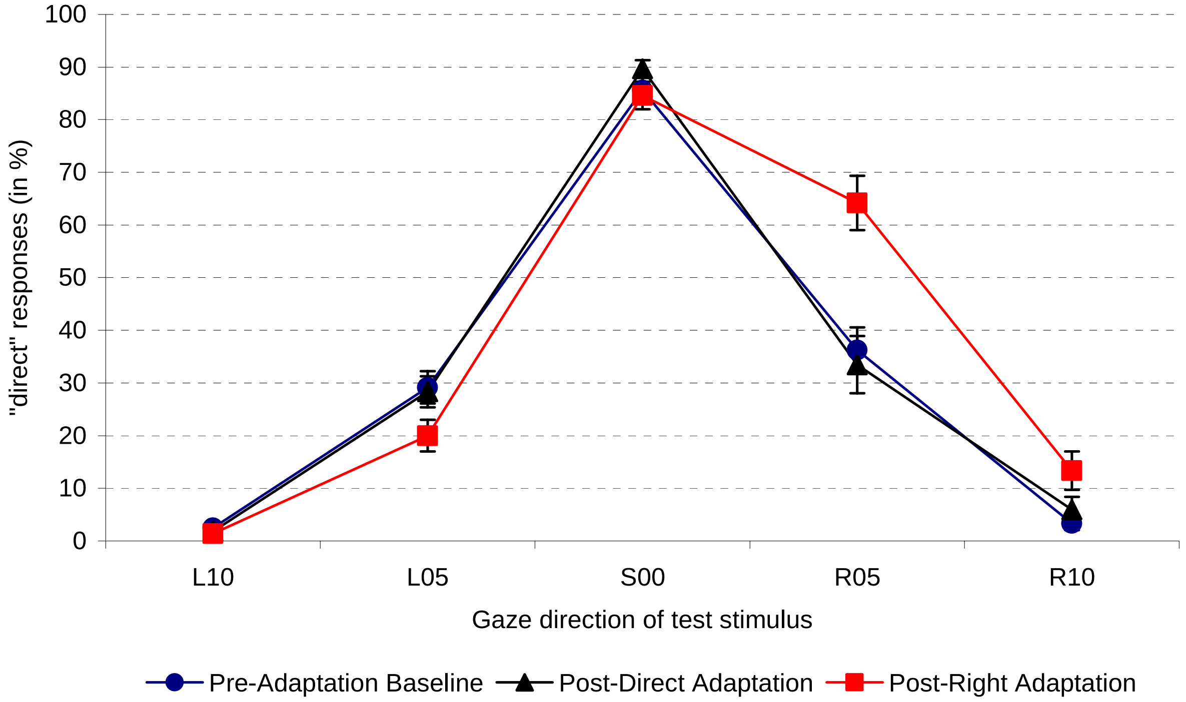


Figure 11: Percentages of "direct" responses (mean across 20 observers) for the five different gaze angles of test faces. Responses are displayed depending on whether test faces were shown before adaptation (blue) or after adaptation to either direct (black) or right (red) gaze direction. Please note the almost identical response pattern obtained in the pre-adaptation and post-direct adaptation tests and the increase of incorrect "direct" classifications of test stimuli with right gaze following adaptation to that direction.

Finally, the responses to trials showing direct gaze were analysed separately. Bonferroni-corrected t tests were conducted in order to examine the classifications of test stimuli with direct gaze after direct and right gaze adaptation, respectively. These analyses revealed that the numerical reduction in correct classifications of direct gaze after right adaptation (*M* = 84.6%) as compared to direct adaptation (*M* = 89.7%) did not reach conventional levels of significance (*p* = .06). However, there was a significant decrease in incorrect "right" classifications of direct gaze following right (*M* =

0.3%) as compared to direct gaze adaptation (M = 2.6%, t[19] = -4.21, p < .05) as well as a significant increase in incorrect “left” classifications following right (M = 14.8%) as compared to direct adaptation (M = 7.0%, t[19] = 3.51, p < .05). For an overview of the results, please see Table 1 and Figure 11.

4.3.2 Electrophysiological Results

For ERPs to test faces, mean amplitudes[1] in the time segment 92 - 132 ms (P100) were analysed at 8 occipitotemporal electrodes (O1, O2, P9, P10, PO9, PO10, TP9, and TP10). Mean amplitudes for time segments 150 - 190 ms (N170), 205 - 245 ms (P2), and 250 – 350 ms were taken at 8 posterior electrodes (P7, P8, TP9, TP10, P9, P10, PO9, and PO10). The time segments were defined by the interval of ± 20 ms placed around the peak latency (defined at the electrode in the grand average where the respective ERP-component was maximal). Finally, mean amplitudes in the time interval of 400 – 600 ms were analysed for electrode locations F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4. Where appropriate, epsilon corrections for heterogeneity of covariances were performed (Huynh & Feldt, 1976). All post-hoc t tests were corrected according to the Bonferroni-procedure (α = .05).

P1

Following the rationale of the analysis of behavioural results, P1 mean amplitudes in response to test faces were first analysed in a repeated measurements ANOVA with Electrode site (O1/O2, P9/P10, PO9/PO10, and TP9/TP10), Hemisphere (left, right), Adaptation condition (direct, right), Deviance (5°, 10°), and Direction of test gaze (left, right) as factors. The analysis revealed a significant main effect of electrode site (F[3, 57] = 44.22, p < .001) and a significant main effect of adaptation (F[1, 19] = 6.37, p < .05).

As there was no interaction of the factors Deviance and Adaptation, mean amplitudes obtained in the conditions L05 and L10 as well as R05 and R10 were col-

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[1] For the clearly pronounced P1 and N170 components all analyses were also performed on peak amplitudes. For P1, peak amplitudes were measured at electrodes O1 and O2 as largest individual positivities in the time window of 90 – 130 ms. For N170, peak amplitudes were individually determined for each participant and hemisphere as amplitudes at the latency of the maximal negative peak between 150 – 200 ms within electrodes P7, P9, PO9, and TP 9 as well as P8, P10, PO10, and TP10, respectively. If not otherwise stated, these analyses led to the same effects as those on mean amplitudes reported here.

lapsed across gaze deviances and further analysed in a new ANOVA with the factors Electrode site, Hemisphere, Adaptation condition, and Direction of test gaze (left, direct, right). This analysis therefore examined the effects of adaptation on the perception of test stimuli of all three gaze directions with an equal number of trials in all three conditions. The analysis revealed significant main effects of site (*F*[3, 57) = 45.25, $p < .001$) and adaptation condition (*F*[1, 19] = 7.67, $p < .05$), reflecting small but significant P1 amplitude differences between trials following direct gaze adaptation ($M = 3.05$ µV) and right adaptation ($M = 2.90$ µV, please see Figures 12 and 13).

The analysis of P1 latencies at electrodes O1 and O2 in both a 2 x 2 x 2 x 2 – ANOVA with Hemisphere, Adaptation condition, Deviance (5°, 10°) and Direction (left, right) as factors and a 2 x 2 x 3 – ANOVA with Hemisphere, Adaptation condition, and Direction (left, direct, and right) revealed no significant effects (all *p*s > .05).

N170

Figures 12 and 13 depict ERPs following adaptation to direct and right gaze direction for test faces with left, direct, and right gaze direction at electrode locations P7, P8, P9, P10, PO9, PO10, TP9, and TP10. Visual inspection suggests that adaptation has small effects on N170 amplitudes, with test faces presented following adaptation to right gaze direction evoking larger amplitudes than test faces presented after adaptation to direct gaze direction. This N170 amplitude effect appears to be strongest, yet only in the range of approximately 0.5 µV, for left gazing test stimuli, weaker for test stimuli with direct gaze direction, and hardly observable in response to right gazing test stimuli. N170 amplitudes were first statistically analysed in a repeated measurements 4 x 2 x 2 x 2 x 2- ANOVA with Electrode site (P7/P8, P9/P10, PO9/PO10, and TP9/TP10), Hemisphere (left, right), Adaptation condition (direct, right), Deviance (5°, 10°), and Direction (left, right) as factors. This analysis revealed a significant main effect of electrode site (*F*[3, 57] = 12.76, $p < .001$), a significant main effect of direction (*F*[1, 19] = 8.48, $p < .01$), and a significant three-way interaction between the factors Electrode site, Adaptation condition, and Direction (*F*[3, 57] = 3.81, $p < .05$).

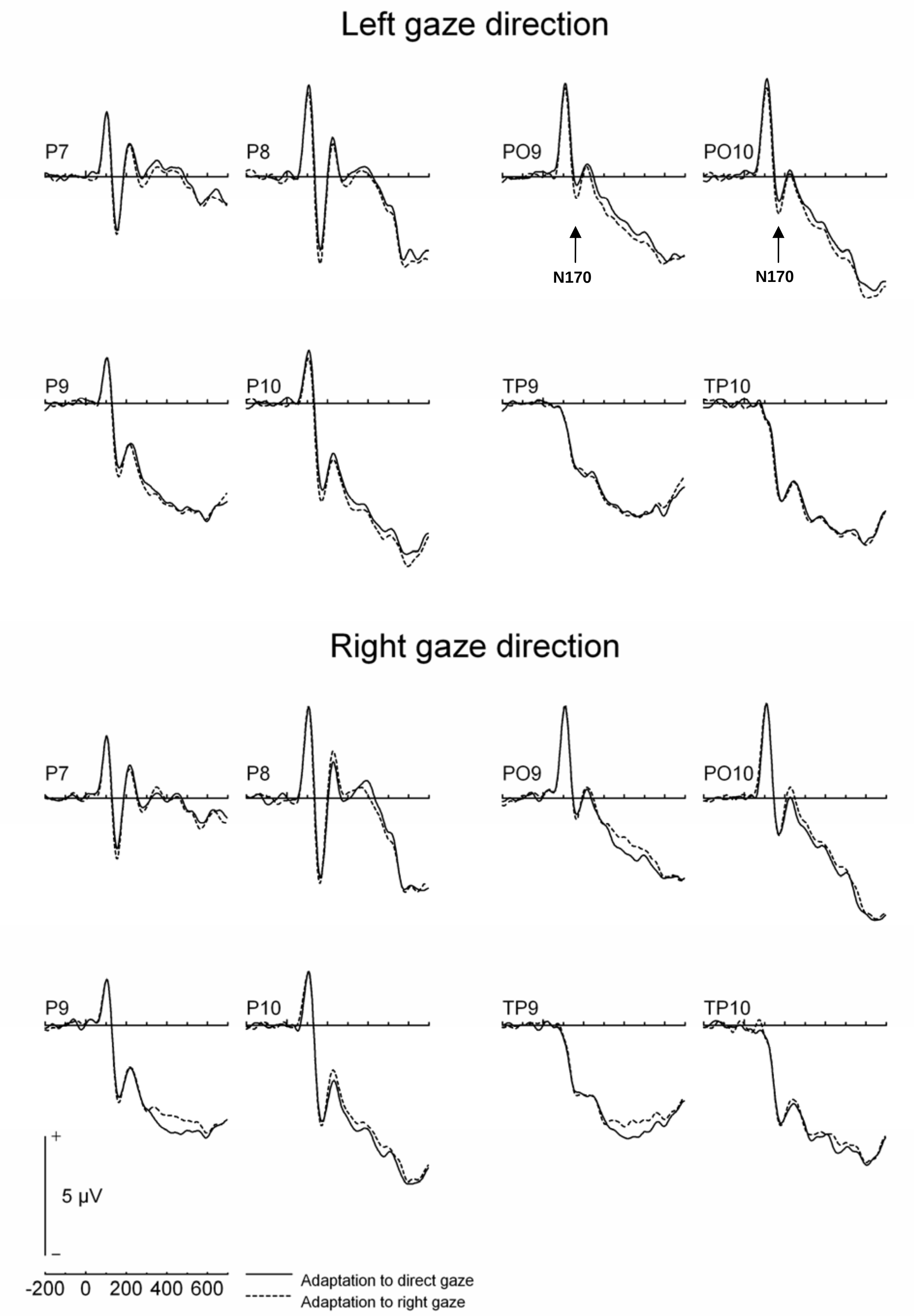

Figure 12: Grand averages over 20 participants collapsed across deviance for ERPs to test stimuli gazing in the left (upper part) or right (lower part) direction after adaptation to either direct (solid lines) or right (dashed lines) gaze direction. Please note the N170 adaptation effect for left gazing stimuli at PO9/PO10 as indicated by arrows.

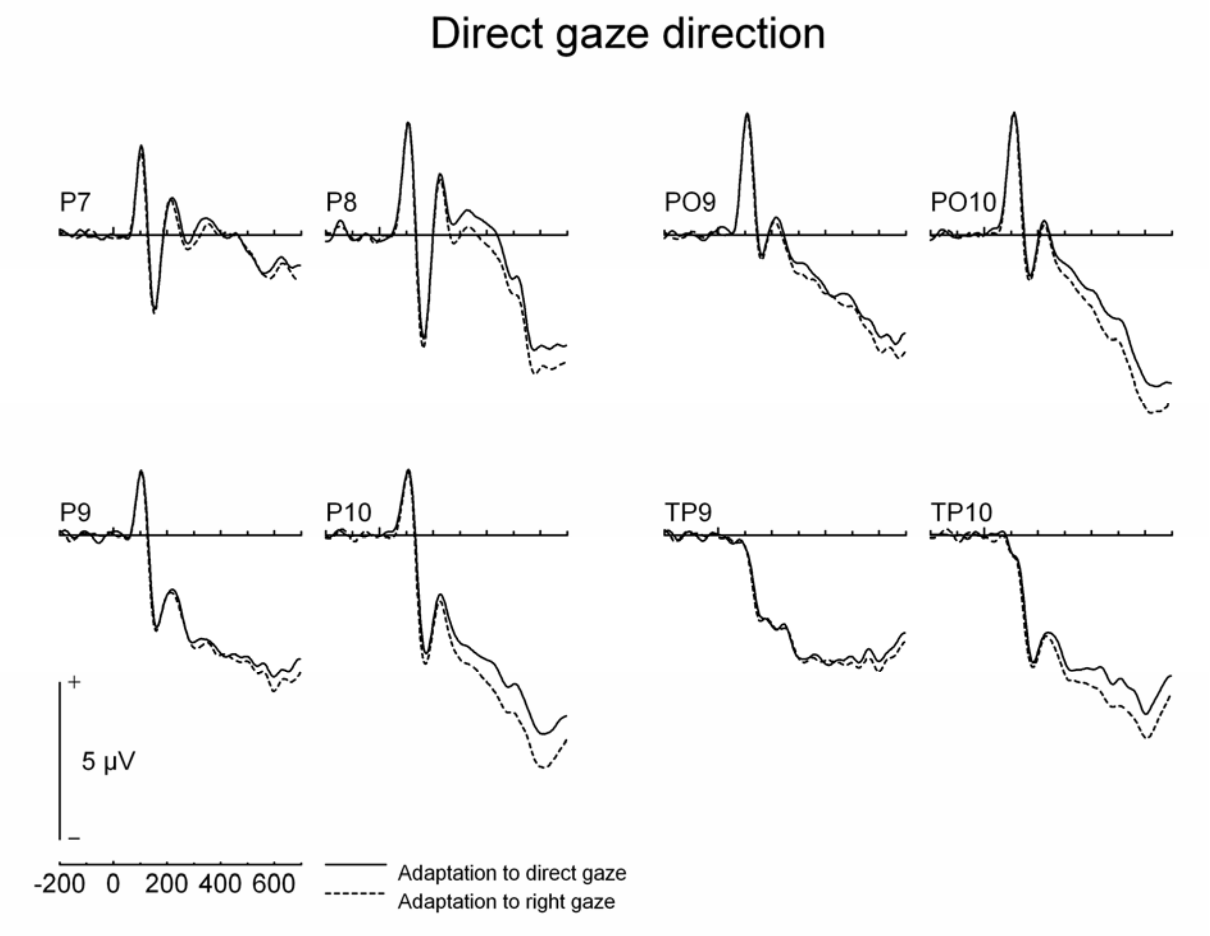

Figure 13: Grand Averages over 20 participants collapsed across deviance, for ERPs recorded in response to test stimuli gazing directly at the observer after adaptation to either direct (solid lines) or right (dashed lines) gaze direction.

Again, the first analysis did not reveal an interaction of the factors Adaptation and Deviance[2]. Therefore, mean amplitudes obtained in the conditions L05 and L10 as well as R05 and R10 were collapsed across gaze deviances and a new ANOVA was calculated with three levels of the factor Direction. This ANOVA on the factors Electrode site, Hemisphere, Adaptation condition, and Direction of test gaze (left, direct, right) revealed significant main effects of electrode site (*F*[3, 57] = 12,43, *p* <

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[2] The corresponding analysis of peak amplitudes, however, revealed a significant four-way interaction of the factors Site, Hemisphere, Adaptation condition, and Deviance (*F*[3, 57] = 3.63, *p* < .05). Separate analyses of Adaptation condition x Deviance for each electrode site revealed a significant main effect of adaptation only for electrode P8 (*F*[1, 19] = 6.26, *p* < .05). However, only visual inspection suggested that the larger N170 amplitude to test stimuli following right adaptation (as compared to direct adaptation) were more pronounced in the 5° condition as compared to the 10° condition (*F*[1, 19] = 2.51, *p* = .13).

.001) and direction (*F*[2, 38] = 3.72, *p* < .05), and a significant interaction of the factors Electrode site, Adaptation condition, and Direction (*F*[6, 114] = 2.62, *p* < .05). To analyse this interaction, separate analyses were conducted for the four different electrode sites with Adaptation and Direction as factors. For P7/P8 the analysis revealed a trend towards a main effect of adaptation (*F*[1, 19] = 3.96, *p* = .06) reflecting larger N170 amplitudes following right (*M* = -2.06 µV) as compared to direct adaptation (*M* = - 1.87 µV, see Figures 12 and 13). At P9/10 the analysis revealed a significant main effect of Direction (*F*[2, 38] = 5.55, *p* < .01) due to significantly larger N170 amplitudes in response to right gazing test stimuli (*M* = -3.37 µV) as compared to test stimuli showing both left (*M* = -3.14 µV, *t*(19) = 3.15, *p* < .05) and direct eye gaze (*M* = -3.15 µV, *t*(19) = 3.26, *p* < .05). At electrodes PO9/10 there was a strong trend towards a significant interaction of the factors Adaptation and Direction (*F*[2, 38] = 3.20, *p* = .05) resulting from the fact that the larger N170 amplitudes following right as compared to direct adaptation only reached a level of significant difference for test stimuli showing left gaze (see Figures 12 and 13). Amplitudes evoked by these test stimuli were significantly larger following adaptation to right gaze direction (*M* = -0.95 µV) as compared to following adaptation to direct gaze (*M* = -0.48 µV, *t*[19] = 2.54; *p* < .05). A separate analysis at electrodes TP9/TP revealed no significant effects (all *p*s > .09).

The analysis of N170 latencies in a 2 x 2 x 2 x 2 - ANOVA with Hemisphere, Adaptation condition, Deviance (5°, 10°), and Direction (left, right) as factors revealed a significant three-way interaction between Hemisphere, Adaptation condition, and Deviance (*F*[1, 19] = 4.78, *p* < .01) due to a significant interaction between Adaptation and Deviance in latencies obtained at left hemispheric (*F*[1, 19] = 5.96, *p* < .05) but not at right hemispheric electrodes (all *F*s < 1). At left hemispheric electrodes N170 latencies evoked by stimuli deviating 10° from direct gaze were significantly delayed (*M* = 164.3 ms) as compared to 5° conditions (*M* = 160.8 ms) when presented after adaptation to direct gaze. Following adaptation to right gaze direction or at electrodes located over the right hemisphere, no such effect could be observed (*F* < 1). As this ANOVA revealed an interaction of the factors Adaptation condition and Deviance, data were not collapsed across deviances for the additional analysis including responses to test stimuli with direct gaze. Instead, data considering these stimuli were analysed in a 2 x 2 x 5 – analysis with Hemisphere, Adaptation, and Direction (5° left, 5° right, 10° left, 10° right, and direct) as factors. This analysis revealed no significant effects (all *p*s >.10).

P2

Figures 14 and 15 depict ERPs in response to test faces with left, direct, and right gaze direction in separate plots for trials following direct and right gaze adaptation, respectively. Visual inspection suggests that right gazing test stimuli elicit smaller P2 amplitudes as compared to direct and left gazing test stimuli following direct adaptation, whereas after adaptation to right eye gaze amplitudes evoked by right gazing test stimuli appear to be larger than those evoked by test stimuli gazing to the left or directly at the observer.

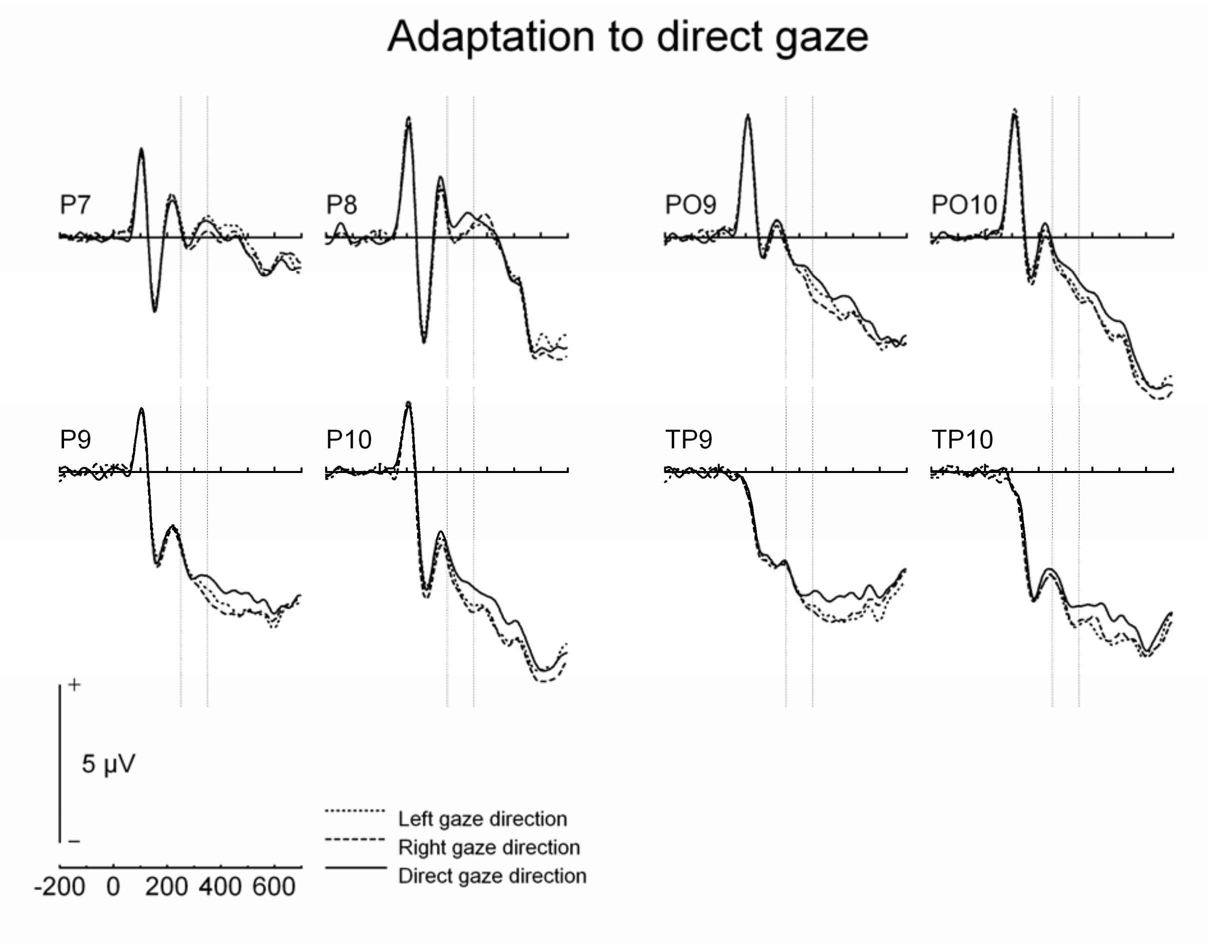

Figure 14: Grand Average ERPs to test stimuli across 20 observers for a selected set of electrodes. Responses to the three different gaze directions (collapsed across deviance) following adaptation to direct eye gaze. Please note the smaller negativity between 250 and 350 ms (vertical lines) evoked by direct gazing test stimuli as compared to test stimuli with left and right gaze direction.

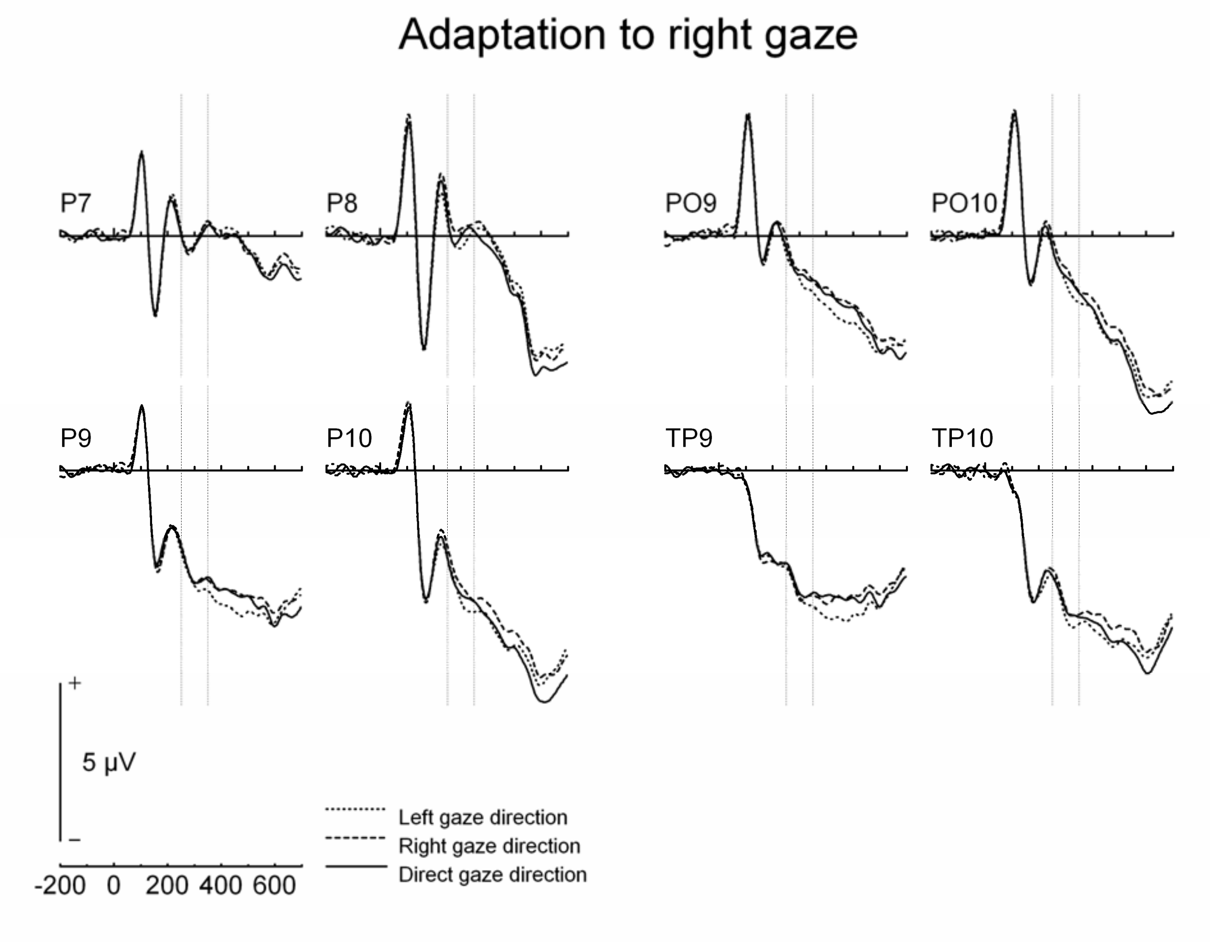

Figure 15: Grand Average ERPs to test stimuli across 20 observers for a selected set of electrodes. Responses to the three different gaze directions (collapsed across deviance) following adaptation to right gaze direction. Please note the smaller negativity between 250 and 350 ms (vertical lines) evoked by right gazing test stimuli as compared to test stimuli with left and direct gaze direction.

In analogy to the earlier components, P2 amplitudes were first analysed in a repeated measurements 4 x 2 x 2 x 2 x 2- ANOVA with Electrode site (P7/P8, P9/P10, PO9/PO10, TP9/TP10), Hemisphere (left, right), Adaptation (direct, right), Deviance (5°, 10°), and Direction (left, right) as factors. This analysis revealed a significant main effect of Electrode site (*F*[3, 57] = 37.50, *p* < .001), a significant two-way interaction of Adaptation and Direction (*F*[1, 19]= 6.84, *p* < .05), a three-way interaction of Site, Hemisphere and Direction (*F*[3, 57] = 3.09, *p* < .05), and a four-way interaction of Electrode site, Hemisphere, Adaptation, and Direction (*F*[3, 57] = 3.49, *p* < .05). As there was no interaction of the factors Adaptation and Deviance, mean amplitudes obtained in the conditions L05 and L10 as well as R05 and R10 were collapsed across gaze deviances. Based on these data, a new ANOVA with the factors Electrode site, Hemisphere, Adaptation, and Direction of test gaze (left, direct, and right) revealed a significant main effect of electrode site (*F*[3, 57] = 37.28, *p* < .001), a two-way interaction of Adaptation and Direction ($F[2, 38] = 3.58$, $p < .05$), and a three-way interaction of the factors Electrode site, Hemisphere, and Direction ($F[6, 114] = 4.05$, $p < .01$). Visual inspection of the mean amplitudes evoked by the three test gaze directions after adaptation to either direct or right gaze suggests that the two-way interaction of Adaptation condition and Direction resulted from smaller, i.e. more negative, P2 amplitudes to right gazing test stimuli ($M = -1.10$ µV) as compared to direct gazing test stimuli ($M = -0.87$ µV) and left gazing test stimuli ($M = -0.96$ µV) following direct adaptation, whereas after adaptation to right eye gaze amplitudes evoked by right gazing test stimuli were larger, i.e. less negative ($M = -0.90$ µV) than those evoked by test stimuli gazing to the left ($M = -1.13$ µV) or directly at the observer ($M = -1.03$ µV, see Figure 14). However, it needs to be noted that the post-hoc *t* tests conducted in order to evaluate the statistical significance of the largest differences observed just failed to reach conventional levels of significance ($t[19] = -2.07$, $p_{\text{uncorrected}} = .052$, for comparison of amplitudes to right and direct gazing test stimuli after direct adaptation, $t[19] = -2.02$, $p_{\text{uncorrected}} = .058$, for comparison of amplitudes to left and right gazing test stimuli after right adaptation). Finally, the interaction between Electrode site, Hemisphere and Direction was further analysed in separate analyses for each electrode site. These revealed a significant interaction of Hemisphere and Direction at electrode site P7/8 ($F[2, 38] = 5.13$, $p < .05$) but not for the other electrode sites (all *p*s > .20). The significant interaction was due to the fact that at electrode P8 (but not at P7) amplitudes in response to test stimuli with direct gaze ($M = 1.44$ µV) were significantly larger than those in response to test stimuli showing left gaze ($M = 1.11$ µV; $t[19] = 2.37$; $p < .05$, see Figures 14 and 15).

250 – 350 ms

Concerning effects of adaptation in a later time interval between 250 ms and 350 ms, Figures 14 and 15 suggest that test stimuli gazing in the adapted direction evoked more positive amplitudes than test stimuli with eye gaze directed in the unadapted directions. This seems to be the case both for test stimuli with direct gaze following direct gaze adaptation and for stimuli gazing to the right following adaptation to right direction.

Mean amplitudes in the time range of 250 - 350ms were analysed in a repeated measurements ANOVA with Electrode site (P7/P8, P9/P10, PO9/PO10, and TP9/TP10), Hemisphere (left, right), Adaptation (direct, right), Deviance (5°, 10°), and

Direction of test gaze (left, right) as factors. The analysis revealed significant main effects of electrode site ($F[3, 57] = 37.10$, $p < .001$) and deviance ($F[1, 19] = 7.92$, $p < .05$), a significant two-way interaction of Adaptation and Direction ($F[1, 19] = 12.63$, $p < .01$), and significant three-way interactions of Electrode site, Hemisphere, and Direction ($F[3, 57]= 11.90$, $p <.001$), Electrode site, Adaptation and Direction ($F[3, 57] = 3.20$; $p <.05$), and Electrode site, Deviance and Direction ($F[3, 57] = 3.50$; $p < .05$). Finally, there was a significant four-way interaction of the factors Electrode site, Hemisphere, Deviance, and Direction ($F[3, 57]= 5.43$. $p < .01$). As the ANOVA did not reveal an interaction of the factors Adaptation and Deviance, mean amplitudes obtained in the conditions L05 and L10 as well as R05 and R10 were collapsed across gaze deviances and a new ANOVA was calculated with three levels of the factor Direction. This 4 x 2 x 2 x 3 ANOVA with the factors Electrode site, Hemisphere, Adaptation, and Direction of test gaze revealed significant main effects of electrodes site ($F[3, 57] = 36.43$, $p < .001$), direction ($F[2, 38] = 4.48$, $p < .05$), a significant interaction of Adaptation and Direction ($F[2, 38] = 9.33$, $p < .01$), and a three-way interaction of Electrode site, Hemisphere, and Direction ($F[6, 114] = 6.02$, $p < .001$).

Visual inspection suggests that the interaction of Adaptation and Direction results from more positive amplitudes in response to test stimuli gazing in the adapted direction as compared to amplitudes evoked by test stimuli gazing in the unadapted directions (see Figures 14 and 15). This effect seems to be especially pronounced following adaptation to direct gaze where test stimuli gazing to the left or right elicit more negative amplitudes than those gazing directly at the observer. A similar pattern of responses seems to arise following adaptation to right gaze direction, although in this case the effect seems to be less pronounced than following adaptation to direct gaze.

T tests further investigating the interaction of Adaptation and Direction supported this observation: following adaptation to direct gaze, stimuli gazing directly at the observer evoked significantly less negative amplitudes ($M = -1.90$ μV) than test stimuli gazing in the left ($M = -2.11$ μV, $t[19] = 2.31$, $p < .05$) and right direction ($M = -2.27$ μV, $t[19] = 4.58$, $p < .001$) which did not produce significantly different amplitudes ($p > .09$). After adaptation to right gaze direction, however, the pattern of results was not as straightforward: whereas test stimuli gazing to the right produced the least negative amplitudes ($M = -2.10$ μV), these did only differ significantly from those evoked by test stimuli gazing to the left (*M* = -2.38 µV, *t*[19] = 3.01, *p* < .01) but not from those evoked by test stimuli with direct gaze direction (*M* = -2.22 µV, *p* > .26).

Late positive component

A pattern of results similar, yet polarity-reversed, to that found in the interval of 250 – 350 ms could also be observed in a later time window at fronto-central, central, and parieto-central electrodes. In the time window of ~400 – 600 ms post stimulus onset, test faces with gaze directed in the adapted direction seem to have evoked less positive amplitudes than faces gazing in unadapted directions both following direct (see Figure 16) and right gaze adaptation (see Figure 17).

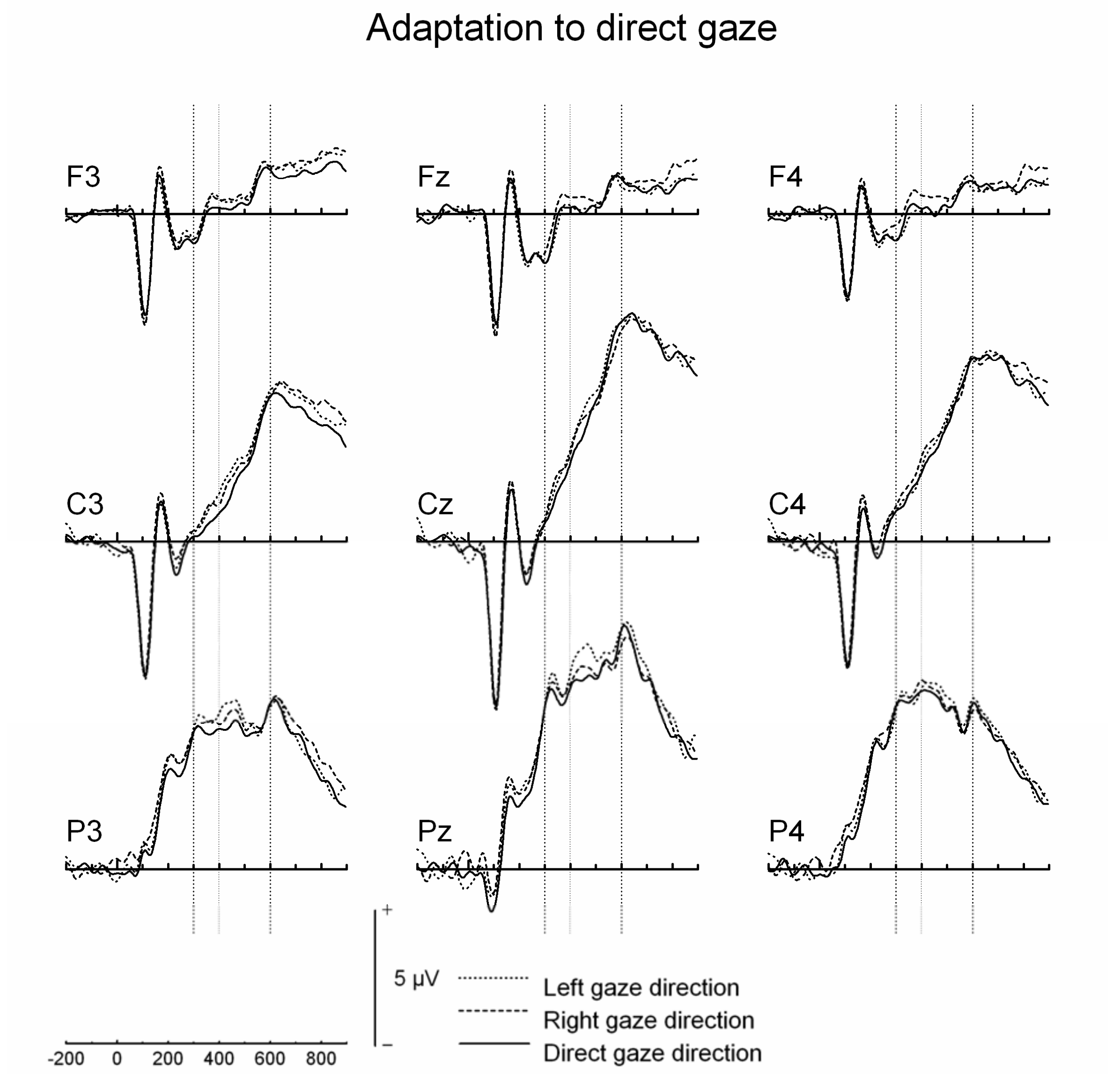

Figure 16: ERPs in response to left (dotted line), direct (solid line), and right (dashed line) gazing stimuli following adaptation to direct gaze. Please note the smaller amplitudes in the time interval of 300 – 600 ms evoked by test stimuli gazing in the adapted (i.e. direct) direction as compared to those evoked by test stimuli gazing in unadapted (i.e. left and right) directions.

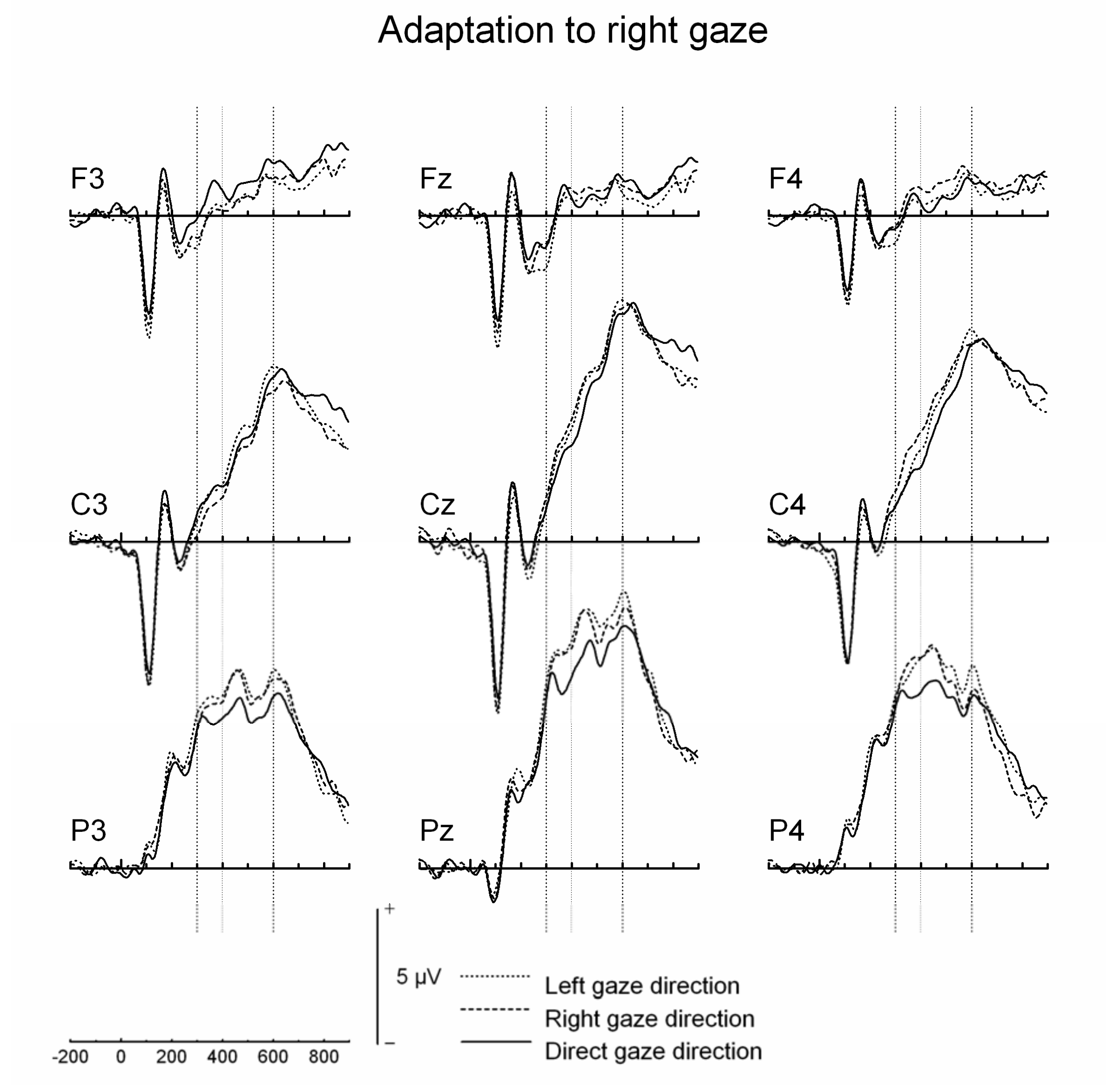

Figure 17: ERPs in response to left (dotted line), direct (solid line), and right (dashed line) gazing stimuli following adaptation to right gaze direction. Please note the smaller amplitudes in the time interval of 300 – 600 ms evoked by test stimuli gazing in the adapted (i.e. right) direction as compared to those evoked by test stimuli gazing in unadapted (i.e. left and direct) directions.

Mean amplitudes evoked by test faces in the time interval between 400 and 600 ms[3] at electrode locations F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4 (see Figures 16

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[3] Please note that differences in the late time interval seem to arise from approximately 300 ms on (see Figures 16 and 17). Therefore, additional analyses were also run for the time interval of 300 – 600 ms. They led to analogous results with a significant interaction of Adaptation and Direction (F[1, 19] = 6.83, p < .01) resulting from significantly smaller amplitudes in response to test stimuli gazing in the adapted as compared to unadapted directions for both the direct (t[19] = -3.77, p < .05 and t[19] = -3.37, p < .05, for comparison of amplitudes evoked by direct gazing test stimuli with those evoked by left and right gaze, respectively) and the right gaze adaptation conditions (t[19] = -3.45, p < .05 and

and 17) were analysed in a repeated measurements ANOVA with Electrode location (frontal, central, parietal), Hemisphere location (left, middle, right), Adaptation (direct, right), Deviance (5°, 10°), and Direction of test gaze (left, right) as factors. This analysis revealed a significant interaction of Adaptation and Direction of test gaze ($F[1, 19] = 5.33$, $p < .05$) which was not further qualified by the factor Deviance ($F < 1$; $p > .09$). Therefore, following the rationale of the preceding analyses, data were collapsed across the factor Deviance and a new analysis was calculated considering direct gaze direction as well as left and right gaze direction. This ANOVA on the factors Electrode location, Hemisphere, Adaptation, and Direction of test gaze (left, direct, right) revealed a significant main effect of direction ($F[2, 38] = 7.09$, $p < .05$) which was qualified by an interaction with Adaptation ($F[2, 38] = 10.56$, $p < .001$). *T* tests were conducted to analyse this interaction. They revealed that following direct gaze adaptation, amplitudes in response to test stimuli gazing in the adapted direction (i.e. directly at the observer) were significantly smaller (i.e. less positive) than those evoked by test stimuli gazing in the left ($t[19] = -4.11$, $p < .05$) or right direction ($t[19] = -3.16$, $p < .05$) which did not differ significantly from each other ($p > .50$, see Figure 16). The same pattern could be observed following right gaze adaptation where responses to test stimuli gazing in the adapted, i.e. right direction, were significantly smaller (i.e. less positive) than those evoked by test stimuli with left ($t[19] = -3.51$, $p < .05$) and direct gaze ($t[19] = -3.10$, $p < .05$) which did not differ significantly from each other ($p > .30$, see Figure 17).

Responses to adaptation stimuli

Additionally, N170 amplitudes in response to the *adaptation* stimuli were analysed (see Figure 18). As described in detail in the method section above, each of the two blocks of test stimuli presented in one adaptation condition was preceded by a series of 24 adaptation stimuli. To analyse the effects of the adaptation procedure itself, the two adaptation series were split into halves, and ERPs to adaptation stimuli presented in the first halves of the two adaptation series were compared to the responses to adaptation stimuli presented in the second halves of adaptation series. Mean amplitudes were analysed in a repeated measurements ANOVA with the fac-

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$t[19] = -2.73$, $p < .05$, for comparison of amplitudes evoked by right gazing test stimuli with those evoked by left and direct gaze, respectively). Amplitudes evoked by test stimuli gazing in directions other than the adapted, however, did not differ significantly from each other (both *p*s > .20).

tors Electrode site (P7/P8, TP9/TP10, P9/P10, and PO9/PO10), Hemisphere (left, right), Adaptation condition (direct, right) and Half (first half, second half). The analysis revealed a significant main effect of electrode (*F*[3, 57] = 4.20, *p* < .06) and a main effect of half (*F*[1,19] = 11.45, *p* < .01) which was due to significantly smaller N170 amplitudes in the second half of the adaptation series (*M* = -2.23 µV) as compared to the first one (*M* = -2.74 µV, see Figure 18). This amplitude reduction from the first to second half of the adaptation series occurred both in the direct and in the right adaptation condition as reflected in the absence of a significant interaction of Adaptation condition and Half (*F* < 1). An analogous analysis of N170 latencies revealed no significant effects whatsoever (all *p*s > .18).

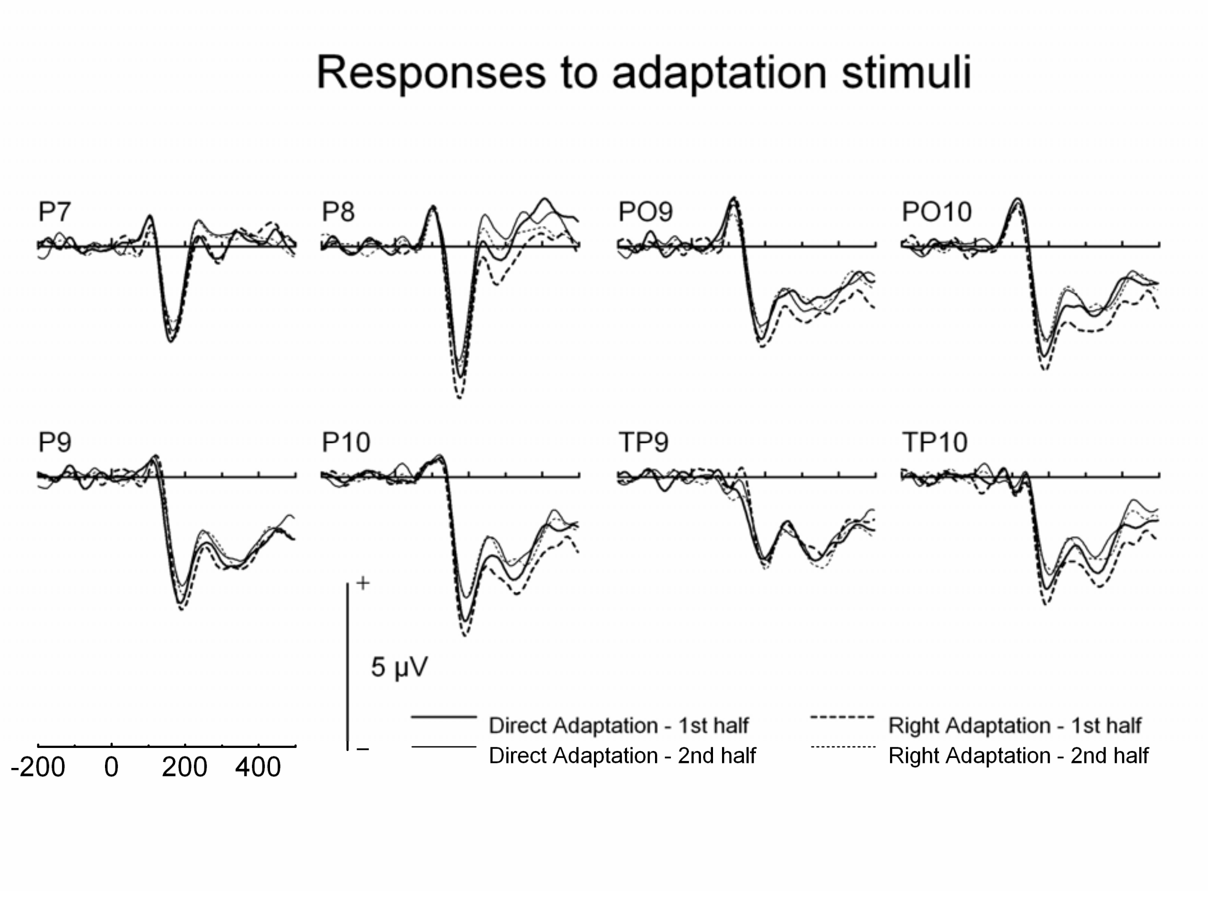


Figure 18: Grand average ERPs in response to *adaptation stimuli* across 20 observers at selected electrodes. Responses to adaptation stimuli with direct (solid lines) and right (dashed lines) eye gaze direction in the first (bold lines) or second (thin lines) halves of the adaptation series. Please note the larger N170 amplitudes evoked by adaptation stimuli presented in the first halves as compared to the second halves.

4.4 Discussion

The current study investigated the effects of adaptation to a relatively small gaze deviation (10° right) on the perception of test stimuli showing similar deviations from direct gaze (10° left, 5° left, direct, 5° right, and 10° right). In order to ensure an equal number of face presentations before each test stimulus, the control condition was designed analogously to the right adaptation condition, therefore consisting of ‘adaptation stimuli’ and ‘top-up’ stimuli with direct gaze. The analysis of the behavioural data revealed no differences between the response patterns obtained in the pre-adaptation condition (which was equivalent to Experiment 1) and the new control condition. This implies that direct gaze represents a neutral point in the representation of gaze direction and does not produce adaptation effects in itself. This could be reconciled with several ERP studies finding the N170 amplitude to be larger in response to eye aversion than in response to direct gaze (Itier et al., 2007a; Puce et al., 2000; Watanabe et al., 2002) suggesting that the processing of averted gaze might require more neuronal resources than does the processing of direct gaze. However, it has to be considered that a consensus on the neural correlates of gaze direction perception has not yet been achieved, as other studies either reported no effects of different gaze directions on the N170 (Taylor et al., 2001) or differences in the opposite direction with direct gaze stimuli evoking larger N170 amplitudes than averted gaze direction (Conty et al., 2007).

The analysis of the behavioural data in the main experiment revealed clear and significant effects of adaptation to right gaze direction on the perception of gaze in test stimuli. Following adaptation, test stimuli gazing both 5° and 10° in the adapted direction were more often perceived as gazing directly at the observer than in the control condition. Further, adaptation to right gaze direction led to a decrease of incorrect ‘right’ classifications and to an increase of incorrect “left” classifications of direct gazing test stimuli – underlining participants’ reduced sensitivity to ‘rightness’ in gaze. Although the magnitude of these gaze adaptation effects was clearly reduced as compared to those obtained in Experiment 1, this is the first evidence for aftereffects of adaptation to eye gaze with a relatively small deviation from direct gaze.

The analysis of the ERP correlates of gaze adaptation revealed a less stringent pattern: although visual inspection suggested that N170 amplitudes were slightly larger following adaptation to right as compared to direct gaze for some gaze directions at some electrodes, the only significant adaptation effect in the N170 time window was reflected in larger amplitudes following right as compared to direct gaze adaptation for test stimuli gazing in the left direction at electrodes PO9 and PO10. Similarly, N170 amplitudes in response to adaptation stimuli seemed to be larger in response to right gaze as compared to direct gaze adaptors. Again, this difference failed to reach significance. There was, however, a significant reduction in N170 amplitudes in the course of adaptation with stimuli presented in the first halves eliciting larger amplitudes than stimuli presented in the second halves both in the direct and right adaptation condition. This underlines the hypothesis that the N170 is sensitive to adaptation to general face information which has been proposed on basis of the findings of Experiment 1. As the N170 is thought to reflect processes related to the structural encodings of faces, it is possible that the adaptation effect in this time window results from a habituation of these face encoding mechanisms.

ERPs in the time range of 250 – 350 ms were affected by adaptation with significantly larger positivity to direct gazing test stimuli following direct adaptation and numerically larger positivity to right gazing test stimuli following right adaptation. These findings underline the sensitivity to gaze adaptation of the processes taking place in this time interval which has also been found in Experiment 1. It is important to consider that the behavioural results obtained in the present study suggest adaptation to direct gaze to not produce any adaptation effects. It should therefore be expected that the ERP results following direct adaptation are not influenced by adaptation but represent the ‘normal’ response pattern obtained for test stimuli of left, direct, and right gaze direction. This pattern does not seem to differentiate between gaze directed in the different directions but rather seems to respond differently when presented with direct vs. averted gaze direction with significantly less negative amplitudes in the former than in the latter case. Interestingly, following adaptation to right gaze which leads to a bias to perceive test stimuli with right gaze direction as gazing directly at the observer, ERPs evoked by right gazing stimuli seem to evoke a similar response pattern as test stimuli with direct gaze without adaptation, i.e. they elicit less negative amplitudes. Test stimuli with direct gaze direction, however, seem to elicit more negative amplitudes when presented following right gaze adaptation (which makes them more likely to be judged as gazing to the left, i.e. diverted direction) than following direct gaze adaptation.

The pattern of ERP correlates of eye gaze adaptation effects was most pronounced in the late positive component (300/400 – 600 ms) over the central and parietal electrodes C3, Cz, C4, P3, Pz, and P4. Here, amplitudes evoked by test stimuli gazing in the adapted direction were significantly less positive than those evoked by test stimuli with eye gaze directed in unadapted directions. The time window and the electrode sites over which this late effect could be observed in the current study as well as the fact that the amplitude increased from frontal to parietal electrodes suggests that it at least partly reflects a P3 effect (Sutton, Braren, Zubin, & John, 1965; for a recent review, see Polich, 2007).

The typical paradigm that has been used in P3 research is the ‘oddball paradigm’ in which two tones are presented that differ with regard to pitch and probability. The participant’s task is to respond to the rare, ‘deviant’ tone, whereas the more frequent or ‘standard’ tone does not require a response. Typically, the ‘deviant’ tones elicit a large positive deflection over parietal electrodes at a latency of approximately 300 ms. The component is usually smaller or absent in response to the ‘standard’ tones. Importantly, the P3 has been shown to emerge not only in response to auditory stimuli but also in visual, somatosensory, and olfactory paradigms and is therefore considered to be modality-invariant (Bernat, Shevrin, & Snodgrass, 2001; Falkenstein, Koshlykova, Kiroj, Hoormann, & Hohnsbein, 1995; Polich, 1999; Sutton et al., 1965). Whereas stimulus modality has been found to be largely irrelevant for the scalp topography of the P3, it has been shown to be of relevance for the amplitude and latency of the component both of which are usually enhanced for visual as compared to auditory stimuli.

Sutton et al. (1965) suggested that the critical feature eliciting the P3 is ‘information delivery’. They assumed that a rare, ‘deviant’ stimulus provides ‘more information’ to the participant than the ‘standard’ stimulus which has to be expected due to the higher frequency of its presentation. Stimulus probability therefore seems to play an important role: the less probable a stimulus is to occur the larger is the information delivery contained in its presentation. Indeed, a 10 – 20 percent probability of target stimulus occurrence has been shown to be the optimal condition to elicit a P3 (Duncan-Johnson & Donchin, 1977) and increasing target stimulus probabilities have been shown to produce decreasing P3 amplitudes (e.g. Polich & Bondurant, 1997).

An alternative theoretical account to explain the P3 effect is the context-updating theory (Donchin, 1981; Donchin & Coles, 1988). This framework proposes that the late positive effect in oddball paradigms reflects a comparison process evaluating the representation of a previous event in working memory and comparing it to a current event. If the comparison does not result in the detection of an attribute change from the previous to the present target, the current mental model of a stimulus is believed to be maintained. However, in the case of an attribute change from the previous to the present target, attentional processes are proposed to run an update of the stimulus representation which is reflected in the larger P3 component towards deviating stimuli.

Considering the context-updating theory of the P3, it seems plausible to assume that the late effect observed in the current study might at least in part reflect the relatively easier processing of a stimulus that most closely resembles the perceptual context provided by the adaptation and top-up stimuli. Stimuli that deviate from that context with regard to their gaze direction might therefore recruit more neural processing resources which is possibly reflected in the larger amplitudes evoked by these stimuli. Considering the proposed theoretical explanations for the P3 effect, it seems plausible to assume that the presentation of test stimuli with their eyes turned in another than the adapted direction might both have a larger informational value and require a more effortful context update than test stimuli gazing in the adapted direction. Due to the design with two blocked presentations of adaptation stimuli for both direct and right gaze adaptation, the presentation of a top-up adaptation stimulus before each test face, and the fact that some of the test stimuli had the same gaze deviances as the adaptation stimuli, there were large differences in stimulus occurrence probability. In the control adaptation condition (i.e. adaptation to direct gaze), for example, 336 of the presented faces had direct gaze direction (48 adaptation stimuli, 216 top-up stimuli, and 72 of the test stimuli) whereas only 144 of the presented test faces gazed in the left or right direction (72 each). One might therefore consider the direct adaptation and top-up stimuli as ‘standard’ stimuli and the presentation of test stimuli gazing in directions different from the adapted one as relatively ‘deviant’.

The observed findings in this late time window therefore closely parallel one of the behavioural consequences of adaptation to specific stimulus attributes which has been described as ‘novelty detection’. The relatively easier processing of stimuli fitting into a current perceptual (and maybe also semantic) context might leave more resources for the processing of stimuli that deviate from that context. This pattern might therefore allow relatively novel stimuli to be processed more thoroughly and allow them to ‘pop-out’, both in terms of the neural resources that they engage and with regard to the novel information that they provide.

5. Experiment 3: The time-course of gaze adaptation

5.1 Introduction

While the time-course of adaptation effects in the perception of basic physical stimulus characteristics has been extensively investigated, high-level face adaptation effects have been detected only in the past few years, and their time-course is only just beginning to be studied. Most recently, the effects of different adaptation durations on the perception of certain aspects of face perception have been investigated showing that the nature of adaptation effects depends on adaptation duration, with short-term and long-term adaptation having differential effects on viewpoint and spatial selectivity (Fang et al., 2007; Kovács et al., 2007, for details on these studies, please see chapters 2.2.2 and 2.2.4). These findings suggest that the systematic variation of adaptation durations can be a tool for the selective adaptation of different neural mechanisms of shape-specific coding.

Leopold, Rhodes, Müller, and Jeffery (2005) explored the dynamics of face adaptation and related them to those of simple aftereffects which are known to be influenced both by the duration of adaptation and the duration of testing (see chapter 2.2.1). The authors tested the dependence of the face identity aftereffect (FIAE) on a wide range of durations of the adaptation (1000 ms to 16000 ms) and test stimuli (200 ms to 1600 ms). In line with traditional aftereffects they found the FIAE to grow stronger as a function of adaptation time and to grow weaker as a function of test duration, i.e. presentation period of the test stimulus.

The present study is motivated in part by the fact that although the influences of adaptor duration and test stimulus duration have been investigated in a few studies, there is only little insight into the influence of the time interval between the presentation of the adaptation and test stimulus on face adaptation effects. Previous studies of face adaptation typically used an adaptor-test interval of just a few hundred milliseconds (Jenkins et al., 2006; Kovács et al., 2006; Leopold et al., 2005; Rhodes et al., 2004; Webster & MacLin, 1999; Webster et al., 2004; but see Leopold et al., 2001, for an informal report of diminished but still measurable face identity aftereffects after an adaptor-test interval of 2400 ms). The idea that face adaptation effects can survive an interval in the range of minutes received preliminary support by a brief report (Carbon & Leder, 2006) on a face distortion aftereffect. As a limitation, this study only used one single face (of *Mona Lisa*), and did not track the decay of the aftereffect. No study to date has precisely evaluated the time-course of face adaptation effects as a function of the adaptor-test interval. In Experiment 1 of the present thesis, the effects of adaptation to left and right gaze directions were investigated in two consecutive blocks with block order counter-balanced across participants. Though separated by a break that offered a number of intervening visual stimuli (e.g. contact with the experimenter, new instruction screen) the data appeared to suggest an influence from gaze adaptors presented in the first adaptation block on performance in the second block several minutes later. This was an accidental finding that was unrelated to the aims of that particular study and was therefore not reported at that stage.

As eye gaze direction often changes quickly in real-life situations of human communication, a finding of relatively long-persisting effects of eye gaze adaptation might be somewhat unexpected. In the current section two experiments will be reported which were specifically designed to gain a systematic evaluation of the time-course of eye gaze adaptation effects. In Experiment 3a, participants' ability to correctly identify direct gaze and gaze directed 5° left or right was measured before and directly after adaptation to eye gaze strongly (25°) diverted to right direction. In order to monitor the decrease of gaze adaptation aftereffects over time, a series of several further post-adaptation phases was run within approximately ten minutes. As prior research (Jenkins et al., 2006; Seyama & Nagayama, 2006) suggested that the magnitude of gaze adaptation effects partly depends on the ambiguity of the test stimulus, the role of the ambiguity of test stimuli for the persistence of the adaptation effects was further explored: Experiment 3b therefore followed the same procedure as Experiment 3a, but using more distinct gaze deviations (10°) in the test stimuli.

5.2 Experiment 3a

5.2.1 Methods

Participants

Twenty-five naïve participants (18 to 30 years, *M* = 21.6 y, 3 men) contributed data and received course credit for their participation. They all reported normal or corrected-to-normal vision and gave their informed consent prior to data acquisition.

Stimuli

Test faces were colour photographs of 6 male and 6 female young adults as in previous studies (Jenkins et al., 2006). Each model posed at gaze angles of 5° left (L05), direct gaze (S00), and 5° right (R05; all directions from the observer's point of view). Photos of the same 12 models gazing 25° right (R25) were used as adaptation stimuli. All faces were presented in a black elliptical mask. Test faces measured 13.0 x 7.5 cm and adaptation faces measured 19.0 x 11.0 cm. Stimuli were presented at a viewing distance of ~87 cm which was kept constant using a chin rest.

Task and Procedure

The experiment began with a *pre-adaptation phase* (see Figure 19, for an overview of the procedure) in order to determine participants' general ability to accurately perceive the gaze direction of faces. Using right index, middle, and ring fingers on three response keys, participants indicated if a test face showed left, direct, or right gaze direction, respectively. Thirty-six test faces (12 identities x 3 gaze directions) were presented in random order. For each trial, a question mark was first presented (800 ms), was then replaced by the test face (400 ms), and followed by a blank screen (2250 ms) during which participants responded. One pre-adaptation trial therefore took 3450 ms, leading to a pre-adaptation phase block duration of two minutes and four seconds (124.2 s).

The pre-adaptation phase was followed by an *adaptation phase* in which participants were presented with two consecutive runs of twelve adaptation stimuli each, presented in randomised order. These stimuli showed eye gaze averted 25° in the right direction and were passively viewed by participants. Exposure duration was 3500 ms for each adaptation stimulus, with an inter-stimulus interval of 200 ms. Adaptation stimuli were presented at about 150% the size of test stimuli so that the eye regions in adaptation and test stimuli were non-overlapping. The adaptation block had a total duration of one minute and 29 seconds (88.8 s).

The adaptation phase was immediately followed by a series of five *post-adaptation phases* during which participants were again asked to determine the direction of eye gaze. In general, *post-adaptation phases* were equivalent to the pre-adaptation phase. The first *post-adaptation phase*, however, was characterised by slight differences in design and duration. Here, each test stimulus was preceded by two consecutive top-up adaptation displays (3500 ms each) presented before the question mark (1000 ms) and the test face (400ms) to ensure maximal adaptation effects during the whole first test block. To avoid any potential effects of immediate facial identity repetitions (Schweinberger, Huddy, & Burton, 2004), neither of the two top-up adaptation stimuli carried the same identity as the following test face. A single trial in the first post-adaptation block had a duration of 10650 ms – the completion of the whole first post-adaptation phase therefore took six minutes and 23 seconds (383.4 s).

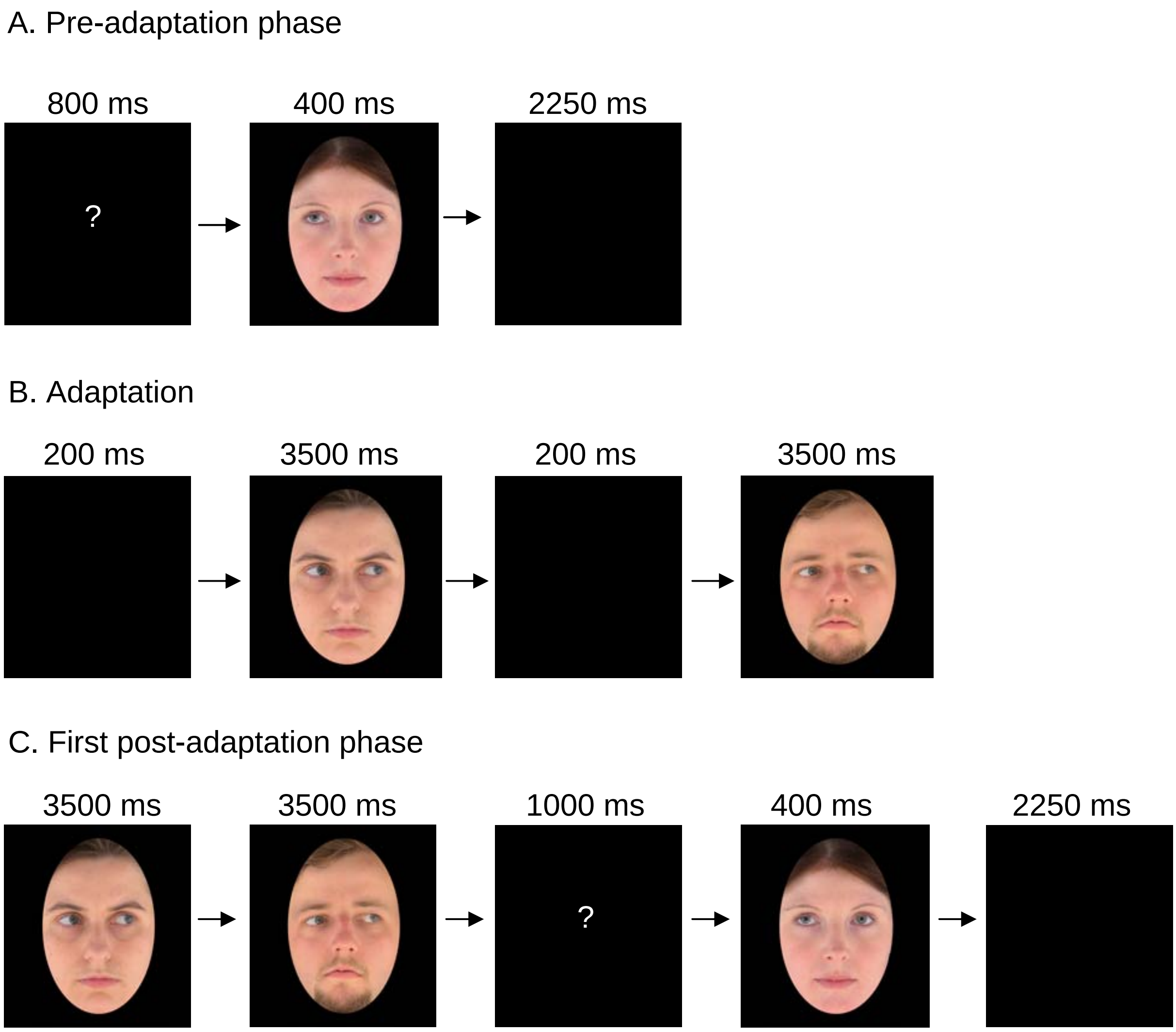


Figure 19: Schematic example for trial procedure in the pre-adaptation (first row), adaptation (second row), and 1st post-adaptation (third row) phases. Please note that test stimuli were actually presented at a smaller size than the adaptors (see Procedure for details) and that the 2nd to 5th post-adaptation trials were equivalent to the pre-adaptation trials.

Participants were then presented with four further *post-adaptation phases* that did not contain top-up adaptation stimuli. The timing parameters of these blocks were equivalent to those of the pre-adaptation phase, with a single trial duration of 3450 ms and a total duration of two minutes and four seconds (124.2 s) for each of the four post-adaptation phases. The consecutive *post-adaptation phases* were separated by standardised breaks of 30 s each, the first of which was presented immediately after the first post-adaptation phase.

The assessment of the temporal persistence of gaze direction aftereffects was a central aim of the current study, and the considerations concerning the analysis of timing were as follows: first, by using top-up adaptation stimuli before each test stimulus, the first post-adaptation phase was designed to capture the maximal adaptation effect in the context of the present study (cf. Jenkins et al., 2006). The starting point in time relative to which the decay of aftereffects was tracked therefore coincided with the end of the first post-adaptation phase (see Figure 20). As practical considerations (limited number of participants, randomised presentation of stimuli in different conditions) prevented an assessment of aftereffects on a trial-to-trial basis, relatively short test blocks were used with only 12 test stimuli for each gaze direction in the second to fifth post-adaptation phase. To determine a time-course of adaptation effects, the average time across all test faces within a given phase (relative to the end of the first post-adaptation phase) was defined as a time point of measurement. Similarly, the average performance across all test faces within a given phase was taken as an indicator of the residual magnitude of aftereffects at this time. Figure 20 illustrates the resulting time scale.

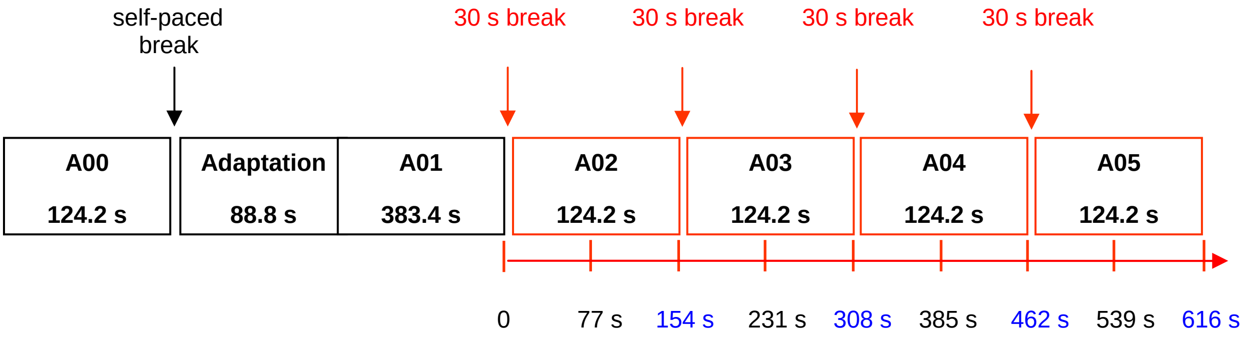


Figure 20: Schematic illustration of time scale. Each box represents one test phase, with “A00” used as an abbreviation for “pre-adaptation phase” and A01 to A05 as abbreviations for the first to fifth post-adaptation phases, respectively. Arrows indicate breaks between blocks which could either be self-paced (black) or standardised for a duration of 30s (red). Times stated in the boxes represent durations of the respective phases. The end of phase A01 is considered to be t=0. Durations printed in blue represent the time elapsed at the end of the respective test phases. Durations printed in black represent the average time elapsed since t=0 across all test faces within a given phase.

5.2.2 Results

In the pre-adaptation test, participants were fairly accurate in discerning eye gaze directions (70.3 ± 22.8%, 71.8 ± 18.9%, and 74.7 ± 18.5% mean correct responses ± standard deviations for left, right and direct gaze, respectively). As expected, the ability to correctly perceive right gaze direction was strongly reduced after adaptation to that direction (9.8 ± 18.1% correct). The correct classification of direct gaze, however, was relatively unaffected (75.3 ± 15.6% correct responses) whereas correct classifications as “left gaze” appeared to increase after adaptation (e.g. to 83.4 ± 23.2% in the first post-adaptation phase). For the detailed response pattern obtained in the different adaptation conditions *(pre-adaptation test, first to fifth post-adaptation test)*, please see Table 2

	left gaze direction			right gaze direction			direct gaze direction		
	„l“	*"r"*	*"s"*	*"l"*	*"r"*	*"s"*	*"l"*	*"r"*	*"s"*
A00	70.3 (4.6)	1.0 (0.7)	28.7 (4.3)	1.7 (1.0)	71.8 (3.8)	26.5 (3.5)	15.1 (3.5)	10.2 (2.6)	74.7 (3.7)
A01	83.4 (4.6)	0.4 (0.4)	16.2 (4.6)	4.2 (2.6)	9.8 (3.6)	86.0 (4.3)	22.9 (3.0)	1.8 (0.7)	75.3 (3.1)
A02	76.4 (3.8)	0.4 (0.4)	23.2 (3.8)	2.4 (1.7)	42.0 (5.2)	55.6 (5.3)	17.9 (2.9)	1.3 (0.8)	80.8 (2.8)
A03	70.9 (3.7)	1.0 (0.6)	28.1 (3.7)	2.3 (1.2)	52.3 (5.4)	45.3 (5.1)	11.6 (3.0)	4.1 (1.9)	84.2 (3.7)
A04	70.1 (3.5)	0.7 (0.5)	29.2 (3.5)	1.0 (0.7)	62.4 (5.0)	36.6 (4.8)	11.7 (2.3)	7.0 (2.1)	81.3 (2.7)
A05	70.7 (4.1)	0.3 (0.3)	29.0 (4.1)	0.7 (0.5)	67.3 (3.4)	32.0 (3.4)	12.1 (2.4)	5.1 (1.6)	82.7 (2.7)

Table 2: Mean percentages (and *SEM*) of “left” (*“l”*), “right” (*“r”*), and “direct” (*“s”*) responses to test stimuli depending on the actual gaze direction of the stimuli (left gaze direction, right gaze direction, direct gaze) and the test phase (A00 to A05). Please note that the pre-adaptation phase is indicated by “A00”, the first to fifth post-adaptation phases are indicated by the abbreviations “A01” to “A05”, respectively.

An analysis of variance (ANOVA) with the factors Adaptation phase (A00, A01, A02, A03, A04, and A05) and Direction of gaze of test stimulus (left, right, and direct) was conducted to analyse the “direct” responses, in analogy to Jenkins et al. (2006). Where appropriate, epsilon corrections for heterogeneity of covariances were performed (Huynh & Feldt, 1976). All post-hoc *t* tests were corrected with the Bonferroni-procedure ($\alpha = .05$).

The ANOVA revealed significant main effects of Adaptation phase ($F[5, 120] = 11.42$, $p < .001$) and Direction ($F[2, 48] = 93.93$, $p < .001$), as well as a significant interaction of these factors ($F[10, 240] = 32.45$, $p < .001$). Whereas the frequency of incorrect “direct” responses to left vs. right test stimuli was comparable in the pre-adaptation phase, there was a dramatic increase in incorrect “direct” responses in the first post-adaptation phase – but only to right gazing stimuli. In subsequent post-adaptation phases, this pattern gradually returned to near-baseline levels. Conversely, there was some decrease in incorrect “direct” responses to left gazing stimuli in the first post-adaptation phase, a pattern that also gradually returned to near-baseline levels subsequently. These observations were further evaluated by post hoc *t* tests, which revealed that whereas the number of incorrect “direct” responses did not differ for left and right gazing stimuli during the pre-adaptation phase ($p>.6$), it clearly did so after adaptation. “Direct” responses were significantly more frequent to right as compared to left gazing stimuli from the first post-adaptation phase up to the third one ($t[24] = 9.74$, $p < .001$; $t[24] = 5.25$, $p < .001$; and $t[24] = 3.36$, $p< .01$, for first, second, and third post-adaptation phases, respectively). This difference was mainly due to a strong increase of “direct” responses to test stimuli showing right gaze direction after adaptation. Compared to the pre-adaptation phase, there were significantly more “direct” responses to right gazing test stimuli in the first ($t[24] = 11.87$, $p < .001$), second ($t[24] = 6.95$, $p < .001$), and third post-adaptation phase ($t[24] = 4.10$, $p < .001$), with a strong trend in the same direction in the fourth post-adaptation phase ($t[24] = 2.26$, $p_{\text{uncorrected}} = .03$). Incorrect “direct” responses to test stimuli showing left gaze exhibited a weaker pattern of aftereffects in the opposite direction: Following adaptation to right gaze, incorrect “direct” responses to left gazing test stimuli significantly decreased compared to pre-adaptation level in the first post-adaptation phase only ($t[24] = -3.01$, $p < .01$). Although some degree of gradual return to pre-adaptation level could also be observed in the data on left gazing stimuli (see Table 2 and Figure 21), differences to pre-adaptation level were not significant in the other post-adaptation phases.

Concerning the classification of stimuli showing direct gaze, there was a very small increase in correct responses after adaptation (see Table 2), which only reached a level of significant difference from the pre-adaptation phase in the third post-adaptation phase ($t[24] = 2.73$, $p < .05$). This enhancement was accompanied by a significant decrease in incorrect “right” classifications of direct gazing test stimuli in the first ($t[24] = -3.68$, $p < .01$), second ($t[24] = -3.53$, $p < .01$), and third ($t[24] = -2.83$, $p < .01$) post-adaptation phases.

Figure 21 depicts the mean percentages of “direct” responses to test stimuli gazing left and right against the time elapsed since adaptation. It was found that the development of the aftereffect over time for left and right gazing test stimuli could be well defined by exponential functions of the form

$$f(x) = (Y_0 - \text{Plateau}) * e^{(-k*x)} + \text{Plateau} \qquad (2)$$

Please see Table 3 for an overview of the parameters of the functions fitted for left and right gazing stimuli, respectively.

	Gaze direction of test face	
Parameter	left	right
Y_0 (in %)	16.17 ± 0.23	84.97 ± 4.76
Plateau (in %)	29.28 ± 0.18	34.87 ± 3.84
k (in 1/s)	0.01011 ± 0.00060	0.00954 ± 0.00309

Table 3: Parameter estimations for exponential functions plotted on the percentages of “direct” responses to test stimuli gazing in the left and right direction, respectively. With Y_0 being the Y value when the time (x) is zero and the plateau being the y value at infinite times. K is the rate constant which is expressed in reciprocal of the X axis time units, in this case in inverse seconds.

There was a high goodness of fit of the exponential functions for both the increase in incorrect “direct” classifications of test stimuli showing left gaze (R^2=0.99) and the decrease in incorrect “direct” classifications of test stimuli showing right gaze (R^2=0.97).

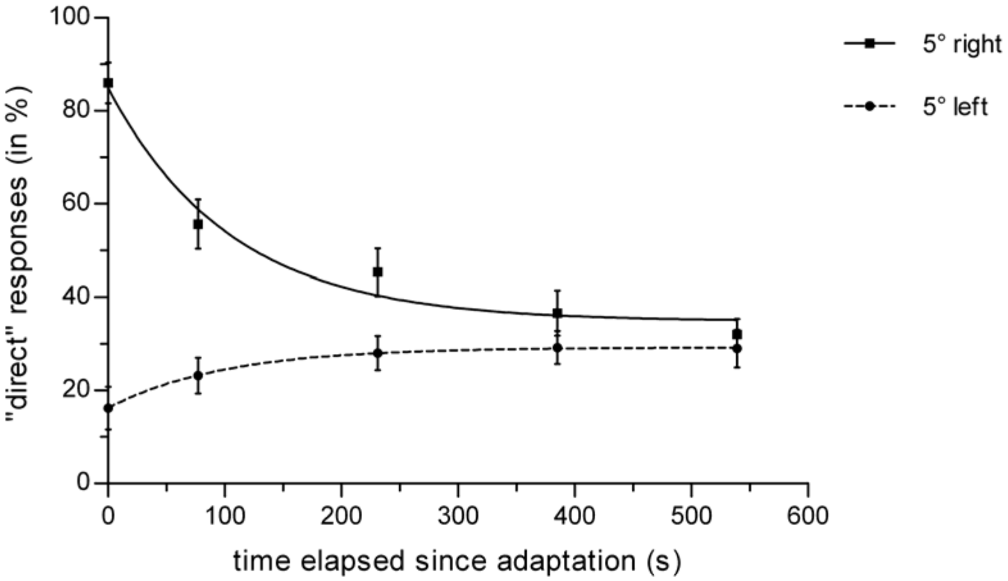


Figure 21: Exponential functions fitted on the percentages of “direct” responses to test stimuli showing left (dotted lines) and right (solid lines) gaze direction.

5.3 Experiment 3b

5.3.1 Methods

Participants

Twenty-five new participants (19 to 32 years old, *M* = 21.4 y, 5 men) contributed data to this study and received course credit for their participation. They all reported normal or corrected-to-normal vision and gave their informed consent prior to data acquisition.

Stimuli

Test faces were colour photographs of the same twelve individuals as in Experiment 3a. The models posed at the gaze angles 10° left (L10), direct (S00), and 10° right (R10), leading to a much more obvious deviance from direct gaze in the ‘left gaze’ and ‘right gaze’ conditions as compared to Experiment 3a. As before, photos of the same 12 models gazing 25° right were used as adaptation stimuli. Stimuli were of the same size as in Experiment 3a and a constant viewing distance of ~87 cm was ensured by using a chin rest.

Task and Procedure

The procedure was equivalent to the one in Experiment 3a.

5.3.2 Results

Participants showed very good accuracy in discriminating left (*M* = 92.9 ± 14.8%), right (*M* = 91.3 ± 16.4%), and direct (*M* = 88.8 ± 12.3%) gaze directions. These accuracies were much higher than those obtained in Experiment 3a (cf. Table 2), reflecting the lower task difficulty. However, the classification of these relatively unambiguous stimuli was also severely altered as a consequence of adaptation, as can be seen in the response pattern depicted in Table 4.

As before, adaptation to stimuli gazing 25° in the right direction severely disrupted the ability to correctly perceive eye gaze in that direction – leading to incorrect “direct” responses in 72.5% (*SD* = 17.9%) of the trials in the first post-adaptation phase. However, this aftereffect seemed to recover more quickly than in Experiment 3a, as incorrect “direct” responses to right test stimuli were already strongly decreased in the second post-adaptation phase (*M* =18.9 ± 25.2%).

	left gaze direction			right gaze direction			direct gaze direction		
	„*l*“	"*r*"	"*s*"	"*l*"	"*r*"	"*s*"	"*l*"	"*r*"	"*s*"
A00	92.9 (3.0)	2.7 (2.3)	4.4 (1.6)	2.3 (1.7)	91.3 (3.3)	6.3 (1.9)	8.1 (2.1)	3.1 (0.9)	88.8 (2.5)
A01	88.0 (4.8)	3.7 (3.3)	8.3 (3.1)	0.7 (0.5)	26.8 (3.7)	72.5 (3.6)	9.6 (2.5)	0.3 (0.3)	90.1 (2.4)
A02	91.0 (4.2)	3.7 (3.7)	5.3 (2.4)	1.3 (1.0)	79.7 (5.5)	18.9 (5.0)	4.3 (1.2)	1.3 (0.8)	94.3 (1.3)
A03	90.0 (4.7)	4.3 (4.0)	5.7 (2.9)	3.0 (3.0)	86.2 (4.9)	10.8 (3.3)	4.7 (1.5)	2.0 (1.0)	93.3 (2.0)
A04	92.7 (4.1)	4.0 (3.6)	3.4 (1.4)	2.3 (2.3)	89.2 (4.7)	8.4 (3.6)	4.0 (1.5)	1.3 (0.6)	94.7 (1.7)
A05	92.2 (4.3)	4.0 (4.0)	3.8 (1.9)	2.2 (1.8)	89.7 (4.4)	8.1 (3.0)	3.7 (1.0)	1.3 (0.8)	95.0 (1.4)

Table 4: Mean percentages (± SEM) of “left” (*“l”*), “right” (*“r”*) and “direct” (*“s”*) responses to test stimuli depending on the actual gaze direction of the stimuli (left, right, direct) and the test phase. Abbreviations as in Table 2.

The ANOVA revealed a significant main effect of adaptation phase (*F*[5, 120] = 74.95, *p* < .001), a significant main effect of gaze direction of test stimulus (*F*[2, 48] = 821.63, *p* < .001), and a significant interaction (*F*[10, 240] = 69.62, *p* < .001). Bonferroni-corrected comparisons showed that the mean percentages of incorrect “direct” responses did not differ for left and right test stimuli during this pre-adaptation phase ($p > .6$). Following adaptation, however, there were significantly more “direct” responses to right as compared to left gazing test stimuli in the first ($t[24] = 16.13$, $p < .001$) and second post-adaptation phases ($t[24] = 3.62$, $p < .01$). These differences between responses to left and right test stimuli were due to a strong increase of “direct” responses to test stimuli showing right gaze direction: compared to the pre-adaptation phase, there were significantly more “direct” responses to right test stimuli in both the first ($t[24] = 19.18$, $p < .001$) and the second post-adaptation phase ($t[24] = 3.02$, $p < .05$). From the third post-adaptation phase on, no such significant post-adaptation effects could be detected (all *p*s > .10). The percentages of “direct” responses to test stimuli showing left gaze did not differ across adaptation phases (all *p*s > .09).

As in Experiment 3a, the mean percentages of “direct” responses were plotted against the time elapsed since adaptation (see Figure 22). The development of the aftereffect over time for right gazing test stimuli could be well defined by an exponential decay function of the form

$$f(x) = (Y_0 – \text{Plateau}) *e^{(-k*x)} + \text{Plateau} \qquad (2)$$

with Y_0 (in %) = 72.54 (± 1.29), Plateau (in %) = 8.99 (± 0.76) and k (in 1/s) = 0.02396 (± 0.00191). It was refrained from fitting the responses to test stimuli showing left gaze, as these did not differ significantly across adaptation phases (see above). In order to allow for a direct comparison with Experiment 3a, the functions of both experiments were plotted together in Figure 22. The exponential decay function fit on the “direct” classifications of test stimuli gazing into the right direction almost perfectly matched the empirical data (R^2=0.99).

As hypothesised, the direct comparison of the results obtained in Experiment 3a and Experiment 3b suggests a much steeper initial decay in the 10° as compared to the 5° experiment.

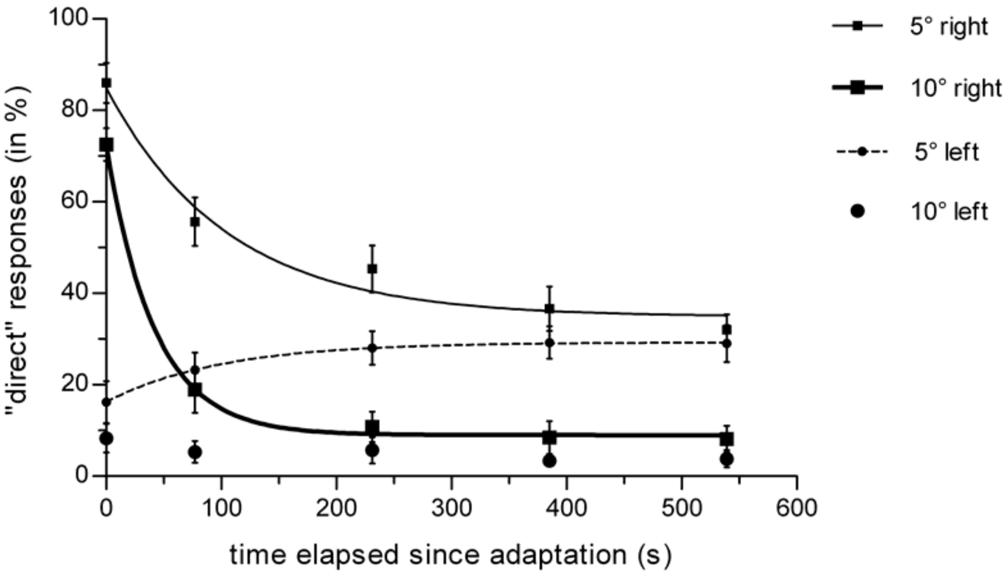


Figure 22: Exponential functions fitted on the percentages of "direct" responses to test stimuli showing left (dashed line) and right (solid line, thin) gaze direction obtained in Experiment 3a (thin lines) and on the percentages of "direct" responses to test stimuli with right gaze direction obtained in Experiment 3b (solid line, bold).

5.4 Discussion

The results of Experiments 3a and 3b replicate recent studies on eye gaze adaptation effects (Jenkins et al., 2006; Seyama & Nagayama, 2006) and the results of Experiments 1 and 2 of the present thesis. Prolonged adaptation to faces showing eye gaze directed to the right subsequently led to an altered perception of eye gaze direction. Most importantly, adaptation biased the classification of eye gaze in the adapted direction to be perceived as direct gaze. For the relatively ambiguous 5° test stimuli this aftereffect decreased over time but remained significant until the fourth post-adaptation phase, corresponding to about 385 s after adaptation (please see Figure 20 for details on the time-course). The time-course of the aftereffect was well modelled by an exponential decay function. Using less ambiguous 10° test stimuli, the adaptation procedure in Experiment 3b led to a qualitatively similar but reduced perceptual bias in the classification of gaze directions. Immediately after adaptation, test stimuli were most often misjudged as looking directly at the observer – even when showing a substantial 10° gaze deviation in the adapted direction. However, this illusionary aftereffect was only measurable in the first and second post-adaptation phases. Based on the time scale of this study this means that the aftereffect lasted about 77 s. The comparison of the exponential decay functions fitted on the empirical data reveals that apart from the higher initial level of illusions in Experiment 3a, there was also a more gradual decrease in these misperceptions in Experiment 3a than in Experiment 3b.

While the time interval between the adaptor and test stimulus has been previously demonstrated to affect the magnitude of aftereffects following adaptation to simple stimulus characteristics such as motion (e.g. Kanai & Verstraten, 2005), the present study is the first to systematically describe the course of high-level adaptation effects over time – from their first maximal level until their decay to insignificance. Although aftereffects caused by adaptation to eye gaze direction showed a systematic decay in post-adaptation phases, a remarkable finding of the present study is that such aftereffects were still measurable several minutes post adaptation. In both experiments, aftereffects of adaptation (i.e. incorrect “direct” classifications of eye gaze in the adapted direction) were maximal immediately following adaptation, and had decayed to near-baseline levels in the last post adaptation phase, approximately after ten minutes. In line with previous research (Jenkins et al., 2006; Seyama & Nagayama, 2006) the initial level of gaze aftereffects was found to be lower for less ambiguous test stimuli. At the same time, adaptation effects on less ambiguous test stimuli were also subject to faster decay.

Experiments 3a and 3b therefore show that adaptation continues to cause biased gaze perception over several minutes, suggesting that these effects may not be limited to very specific conditions in the laboratory. Instead it seems likely that, under appropriate conditions, adaptation may bias the social perception of eye gaze in real-life situations. Face adaptation effects have been investigated for a multitude of social signals, some of which are typically subject to relatively rapid changes (e.g. eye gaze direction, expression, facial speech), whereas others (e.g. gender, identity) tend to be more stable over time. Invariant vs. changeable aspects of human faces are thought to be processed in different neural systems (Haxby et al., 2000). A plausible but yet unexplored hypothesis would be that the recalibration processes evident in adaptation effects are faster for those systems coding changeable aspects of facial information. While recent research has begun to demonstrate different mechanisms for short- and long-term adaptation (Fang, Murray, & He, 2007; Kovács et al., 2007), an important further question for future research will be whether both mechanisms and time-courses of adaptation effects can be dissociated for different social signals in faces. Tentative support for this assumption might be seen in a comparison of the present findings with those by Carbon, Strobach, Langton, Harsányi, Leder, and Kovács (2007) who reported residual aftereffects of adaptation to distorted faces to be still measurable 24 hours after adaptation. These authors measured effects at only one point in time, and a precise tracking of the decay of aftereffects to invariant vs. changeable aspects of faces will therefore be required for a more thorough comparison.

As this is the first study to systematically determine the effects of the adaptor-test-interval in high-level face adaptation, it is difficult to relate the findings of Experiment 3a and 3b to those of earlier studies. However, the comparison of the current data with findings on the decay of MAEs suggests a comparatively long-lived nature of gaze adaptation aftereffects. While the exponential nature of the decay function has typically been reported for simple adaptation effects as well (e.g. Hershenson, 1989; Petersik, 2002; Tootell et al., 1995), Hershenson (1989) reported that motion aftereffects induced by extensive adaptation durations as long as 15 minutes almost completely decayed only 80 s after adaptation. Finally, whereas the combined effects of adaptor duration and test stimulus duration have been addressed by two previous studies (cf. Leopold et al., 2005; Rhodes et al., 2007), the combined effects of all three factors remain an important issue for future research.

6. Experiment 4: Neural correlates of gender adaptation

6.1 Introduction

Following the prolonged viewing of a female (or male) face participants tend to classify subsequently presented gender-ambiguous faces as distinctively male (or female, Webster et al., 2004). This negative gender aftereffect has been shown to be orientation-contingent, i.e. after adaptation to upright female and inverted male faces, gender-ambiguous faces are more likely to be classified as male when presented in upright orientation and as female when presented in inverted orientation (Rhodes et al., 2004). In a hemifield stimulation paradigm, Kovács et al. (2005) found that gender adaptation effects consist of a position-specific and a position-invariant component. Adaptation to face gender caused strong perceptual aftereffects even when adaptor and test stimulus were presented in different visual hemifields. The magnitude of the aftereffect, however, was significantly greater when adaptor and test stimulus were presented in overlapping spatial locations.

In an ERP study, Kovács et al. (2006) further investigated the nature of gender adaptation effects aiming at answering three important questions. First, the authors investigated the electrophysiological correlates of gender adaptation. As high-level aftereffects have been found to be largely invariant to changes in the low-level properties of the face stimuli, the authors hypothesised the face-sensitive N170 component, which is thought to be a correlate of the structural encoding of faces, to be the major ERP component reflecting the effects of selective adaptation to gender stimuli. Second, the authors questioned whether high-level gender adaptation could also be found in the perception of complex visual stimuli other than faces, in this case in the perception of human hands. Finally, the authors were interested in investigating the possibility of cross-categorical effects, i.e. when a hand served as adaptation stimulus and a face was used as test stimulus or vice versa.

In order to answer these questions, Kovács et al. (2006) had participants adapt to photographs of female faces, female hands, or control stimuli (Fourier phase randomised versions of the adaptors). In line with the findings of Webster et al. (2004) the behavioural results showed that prolonged adaptation to female faces as compared to control adaptation stimuli led to a bias to perceive subsequently presented morphed faces with different proportions of male and female characteristics as more masculine. Interestingly, the same adaptation effects could also be observed for female hands. However, the authors did not find aftereffects when the adaptor and test stimulus belonged to different categories, strongly suggesting that gender adaptation effects are category-specific. The analysis of the effects of adaptation on the N170 component revealed that adaptation to both hands and faces resulted in a strong and category-specific modulation of the N170. The amplitude of the component was reduced and the latency was increased after adaptation to faces and hands as compared to control stimuli. The adaptation effect on the N170 amplitude was significantly larger over the right than left hemisphere and over parietal than over occipital electrodes. To sum up, Kovács et al. (2006) suggested that the modulation of the N170 component induced by face adaptation might be regarded as a primary correlate of the shape-selective visual adaptation in humans.

Based on the findings of Experiments 1 and 2 reported above, the possibility must be considered that the effects observed by Kovács et al. (2006) might partly be due to the chosen control condition resulting in adaptation to face structures in the gender adaptation condition but not the control condition. In Experiment 1 of the present thesis, N170 amplitude reductions were observed in both gaze adaptation conditions irrespective of the direction of adaptation, whereas there was no such finding after the implementation of a new control adaptation condition in Experiment 2. Therefore, it might be plausible to attribute at least parts of the N170 amplitude reduction observed by Kovács et al. (2006) to the fact that test stimuli were preceded by a face (or hand) stimulus in face (or hand) adaptation trials, which was not the case in the control condition. The use of Fourier phase randomised versions of face and hand adaptors as control stimuli during the adaptation phase led to a different number of face (or hand) presentations preceding the test stimuli in the gender adaptation and control conditions.

In order to test this hypothesis and to disentangle the respective influences of stimulus category repetition and gender adaptation on the N170 reduction, Experiment 4 was designed to replicate the study by Kovács et al. (2006). However, rather than using a completely different image structure in the control condition, faces that were neutral with respect to gender and therefore without any adaptive power (androgynous faces) were used as control stimuli.

Further, Experiment 4 aimed at investigating the category-specificity of gender adaptation effects. It was tested whether the category-specificity of the gender adaptation effect observed by Kovács et al. (2006) would also apply to cross-modal adaptation to gender in voices and faces. In everyday life, we often perceive human faces and voices simultaneously, and we can usually classify both faces and voices as being male and female quite easily. It can therefore be speculated that gender information is much more important in the perception of human voices than hands and that the categorisation of gender in faces might be more susceptible to voice gender information. Moreover, the perception of gender in human voices has recently been shown to be altered as a consequence of adaptation (Schweinberger et al., 2008).

To summarise, the second major goal of the study is therefore to extend the findings on category-specificity of gender adaptation of Kovács et al. (2006) by investigating if adaptation to male voices has an effect on the perception of subsequently presented gender-ambiguous faces.

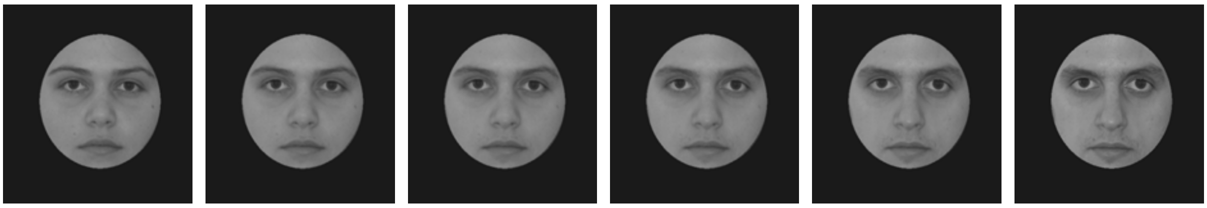
6.2 Methods

Participants

19 naïve and healthy participants (3 men, age range: 19-28 years, *M* = 22.9 y) contributed data to the study. They all reported normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971).

Stimuli

Face stimuli were derived from grey-scale full-front digital photographs of four young males and four young females and had been used in previous studies (e.g. Kovács et al., 2006). Faces had no visible gender-specific features such as facial hair, jewellery, or make up and did not wear glasses. They were fitted behind an oval mask hiding the outer contours of the faces. Morphs were generated by entering male-female pairs into a morphing algorithm (Winmorph 3.1; for details of the morphing procedure please see Kovács et al., 2006). For each pairing, the morphing procedure resulted in 100 face images, varying gradually on a male-female axis. From these images, 4 androgynous face images (50% male/50% female) and 4 male face images (98% male/2% female) were chosen to serve as androgynous and male adaptors, respectively. Four faces with different morph levels (20%/80%, 40%/60%, 60%/40%, and 80% male/20% female ratio) were chosen from each male-female pair and served as the 16 test stimuli (see Figure 23). Both visual test and adaptation stimuli measured 6.5 x 6.5 cm. All face stimuli were presented on a black screen at a viewing distance of ~87 cm which was kept constant using a chin rest.



20% male 40% male **50% male adaptor** 60% male 80% male **98% male adaptor**

Figure 23: Example for test stimuli (20%, 40%, 60%, and 80% male) and androgynous (50% male) and male adaptation stimuli (98% male) derived from the morphing continuum of one female/ male – pairing.

Voice stimuli were generated on the basis of high-quality audio recordings obtained from four male and four female speakers pronouncing the vowel-consonant-vowel (VCV) combination /aba/. All of them were native speakers of German with age ranging from 20 to 27 years. Voices were recorded at a resolution of 16 bit and a sampling rate of 44,100 Hz. Using Adobe Audition™, stimuli were normalised for average amplitude and timing and edited to a uniform duration of 886 ms, containing the normalised 686 ms utterance of the VCV plus 100 ms silence at the beginning and the end, respectively. These pre-processed voices were combined to four male-female voice pairs which were entered into a morphing algorithm (Kawahara & Matusi, 2003). Pairings were matched according to maximal similarity in intensity patterns in the spectrogram in order to optimise morph quality. From each morphed series, 4 androgynous utterances (50% male/ 50% female) and 4 male utterances (100% male) were chosen to serve as androgynous and male acoustic adaptors, respectively. Each VCV utterance was repeated four times to form one single voice adaptor, which led to a total duration of 3544 ms for one acoustic adaptor. For more details concerning the voice stimuli used in this study, please see Schweinberger et al. (2008). Acoustic stimuli were presented via Sennheiser headphones with an approximate intensity of 60 dB along with a black screen.

Apparatus

The EEG was recorded from 32 Ag/AgCl electrodes (AC, 0.05 – 40 Hz, 250 Hz sampling rate) at locations Fz, Cz, Pz, Iz, Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10, PO9, and PO10, with TP10 as initial common reference, using an Easy-Cap$^{\mathrm{TM}}$. Electrode impedances were kept below 10 kΩ. The horizontal electrooculogram (EOG) was recorded from the outer canthi of both eyes, and the vertical EOG was monitored bipolarly from above and below the right eye. Trials with non-ocular artifacts were discarded. For all other trials, the EEG was corrected for contributions of vertical and horizontal eye movements using BESA's automatic EOG artifact correction based on an adaptive artifact correction (Ille et al., 2002). Data were segmented into trials of 1200 ms (200 ms pre-stimulus baseline), digitally low-pass filtered at 20 Hz (zero phase shift, 12 dB/oct), and recalculated to average reference.

Task and Procedure

In a within-subject design participants underwent four adaptation conditions which were either unimodal (face adaptors) or cross-modal (voice adaptors) and either contained ambiguous gender information (androgynous adaptation) or unambiguous gender information (male adaptation). The four different adaptation conditions were tested in separate blocks with order of modality of adaptation stimuli counterbalanced across participants. Within each modality, subjects always adapted to androgynous gender first because this condition was considered to serve as the neutral control condition. As the time-course of gender adaptation effects has not yet been systematically examined, male adaptation trials were always presented following androgynous adaptation in order to avoid a potential influence of the previous adaptation block on the following one (see Experiment 3). In each of the four conditions, 8 repetitions of each of the 4 morphlevels derived from the 4 identity pairings were presented leading to a number of 128 trials per condition.

In each trial, the adaptor was first presented for 3544 ms. It was then replaced by a white question mark on black screen for 800 ms which indicated that participants had to respond to the following test face which was presented for 200 ms. After that, a black screen was shown for 2000 ms, during which participants responded. Participants were asked to determine the gender of the test faces, classifying them as either male or female by pressing one of two marked keys (labelled “M” and “F”) on a standard keyboard. Please see Figure 24, for an overview of the procedure.

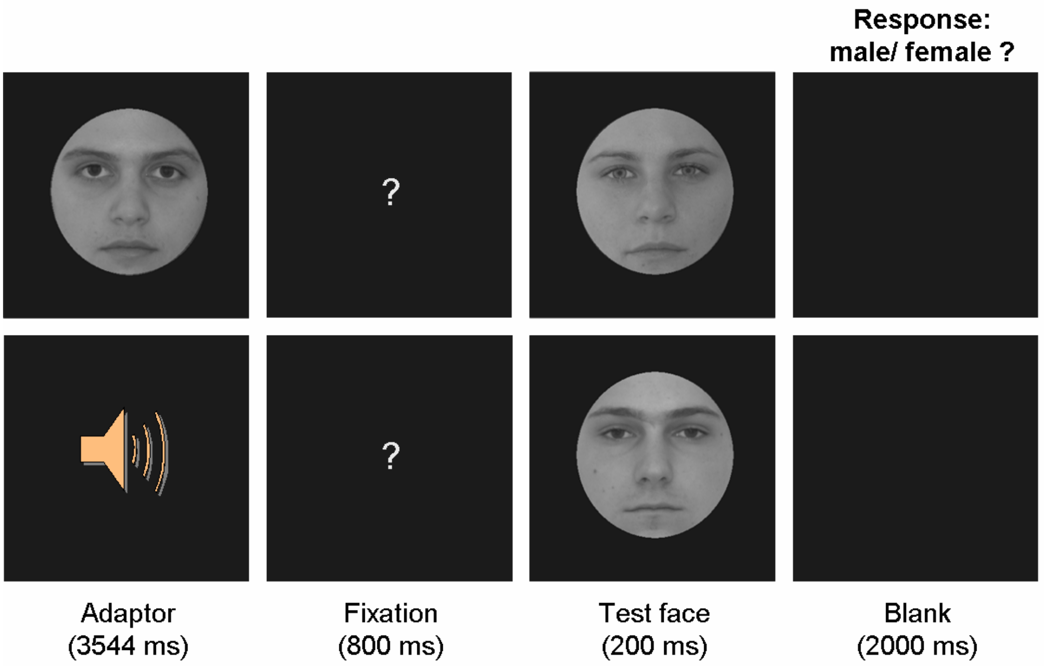


Figure 24: Trial procedure in face adaptation (upper row) and voice adaptation (lower row) trials. Please note that both voice and face adaptors could either be of male or androgynous gender.

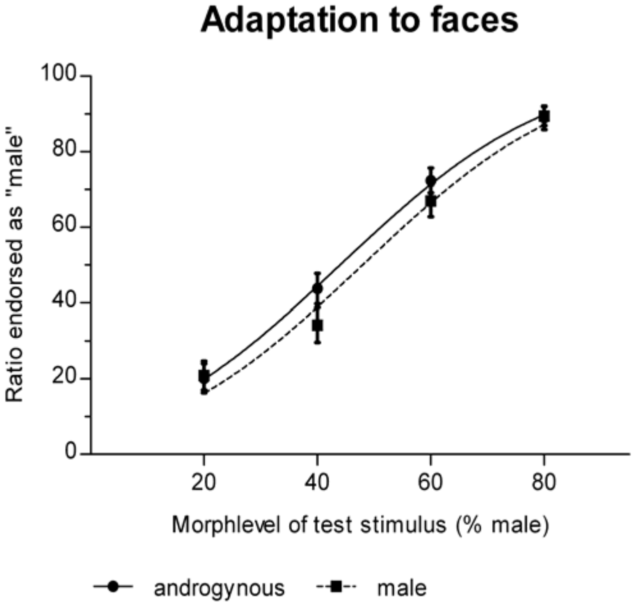
6.3 Results

6.3.1 Behavioural Results

Visual inspection revealed clear adaptation effects for test faces of relative gender-ambiguous morph levels for both the face adaptation condition (see Figure 25 a and Table 5) and the voice adaptation condition (see Figure 25 b and Table 5). Following male adaptation test faces with 40%/60% and 60% male/40% female proportions were less often classified as “male” than following androgynous adaptation, irrespective of the adaptor modality. To determine the statistical significance of these observations, mean percentages of “male” responses for each participant and each condition were analysed in a three-way repeated measurements ANOVA with Modality of the adaptor (visual, acoustic), Gender of the adaptor (androgynous, male), and Morphlevel of test stimulus (20%/80%, 40%/60%, 60%/40%, and 80% male/20% female ratio) as within-subject factors. The analysis revealed a significant main effect of Gender ($F[1, 18] = 5.08$, $p < .05$), a main effect of Morphlevel ($F[3, 54] = 180.43$, $p < .001$), and a significant interaction between these factors ($F[3, 54] = 4.50$, $p < .01$). The ANOVA revealed no further significant effects, in particular no interaction of Modality and Gender ($F[1, 18] = 4.80$, $p > .80$), and Modality, Gender, and Morphlevel

(*F*[3, 54] = 39.27, *p* >.30), although there was a strong trend for an interaction of Modality and Morphlevel (*F*[3, 54] = 2.55, *p* = .066).

a)



b)

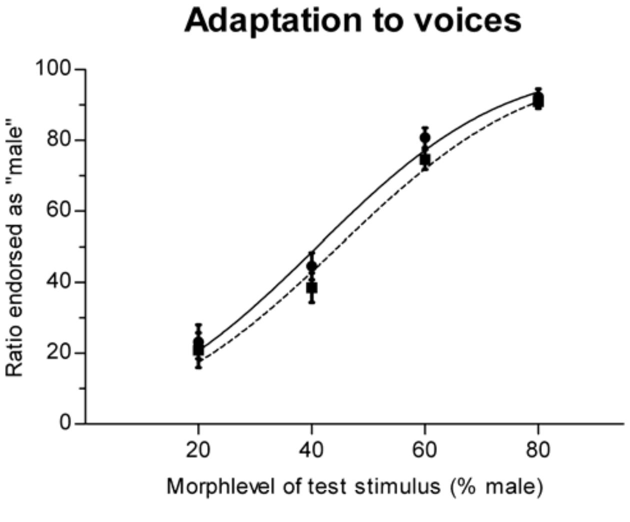


Figure 25: Cumulative Gaussian functions fitted on the behavioural adaptation effects. a) Effects of adaptation to face gender b) Effects of adaptation to voice gender. Solid lines represent results of adaptation to androgynous gender, dashed lines represent results of adaptation to male gender.

T tests collapsed across adaptor modality revealed that the interaction of Gender and Morphlevel resulted from significantly fewer male classifications following male as compared to androgynous adaptation for morphlevels 40%/60% (*t*[18] =

3.31, *p* < .01) and 60% male/40% female (*t*[18] = 2.52, *p* < .05) but not for the morphlevels 20%/80% and 80% male/20% female (both *p*s > .70).

Considering earlier studies which did not find cross-categorical (Kovács et al., 2006) or cross-modal (Schweinberger et al., 2008) effects in gender adaptation paradigms, further analyses aimed at a deeper evaluation of the cross-modal nature of the adaptation effect. Although the analysis described above did not reveal a significant interaction of Modality, Gender, and Morphlevel, further analyses were therefore conducted in order to separately analyse the effects of face and voice adaptation. For face adaptation blocks, a repeated measurements ANOVA with the factors Gender (androgynous, male) and Morphlevel (20%/80%, 40%/60%, 60%/40%, and 80% male/20% female ratio) on the percentage of “male” classifications revealed a significant main effect of morphlevel (*F*[3, 54] = 134.43, *p* < .001) and a significant interaction of Gender and Morphlevel (*F*[3, 54] = 4.87, *p* < .01). *T* tests revealed that the latter was due to significantly fewer “male” classifications following male as compared to androgynous adaptation for test faces of the morphlevel 40% male/60% female (*t*[18] = -3.54, *p* < .01). Although a similar, yet smaller, decrease in the number of “male” responses following adaptation to male faces could be observed for test faces of the morphlevel 60% male/40% female (see Table 5), this difference failed to reach significance (*p* > .20).

Adaptation stimulus	**Morphlevel of test stimulus (% male)**			
	20%	**40%**	**60%**	**80%**
Androgynous face	20.2 (3.8)	43.8 (4.0)	72.4 (4.3)	89.0 (3.1)
Male face	20.9 (3.8)	34.2 (4.6)	66.9 (4.2)	89.4 (2.5)
Size of aftereffect for face adaptation	**-0.7**	**9.6**	**5.5**	**-0.4**
Androgynous voice	23.2 (4.8)	44.6 (3.8)	80.8 (2.8)	92.3 (2.3)
Male voice	20.9 (4.9)	38.5 (4.2)	74.6 (2.8)	90.9 (1.9)
Size of aftereffect for cross-modal adaptation	**2.3**	**6.1**	**6.2**	**1.4**

Table 5: Proportion of mean “male” classifications and size of the aftereffect (difference between number of male classifications following androgynous and male adaptation) depending on the morphlevel of the test stimulus (20% male, 40% male, 60% male, and 80% male) and the adaptation condition (androgynous face, male face, androgynous voice, and male voice).

An analogous separate ANOVA analysing the effects of voice adaptation on the perception of gender in test faces of the different morphlevels revealed a main effect of morph level ($F[3, 54] = 183.76$, $p < .001$) and a trend towards a main effect of gender ($F[1, 18] = 3.05$, $p = .098$). Most importantly, there was no significant interaction of Gender and Morphlevel ($F[3, 54] = 1.37$, $p > .20$). This finding was somewhat surprising, considering that the overall analysis of behavioural data with Modality of the adaptor as a factor did not reveal a three-way interaction of Modality, Gender, and Morphlevel.

Therefore, in order to fully understand the data, additional *t* tests were conducted to compare the number of “male” classifications following androgynous and male adaptation for each of the four morphlevels, respectively. These *t* tests revealed significantly fewer “male” classifications following male compared to androgynous adaptation for test faces of the morphlevel 60% male/40% female ($t[18] = -2.70$, $p < .05$) whereas the similar difference observed for test faces with 40% male/ 60% female ratio was reduced to insignificance ($t[18] = -1.86$, $p = .08$, see also Table 5).

6.3.2 Electrophysiological Results

For ERPs to test faces, mean amplitudes[4] were calculated in the time segment 100 - 140 ms (P100) at 8 occipitotemporal electrodes (O1, O2, P9, P10, PO9, PO10, TP9, and TP10). Mean amplitudes for time segments 150 - 190 ms (N170) and 192 - 232 ms (P2) were analysed at 8 posterior electrodes (P7, P8, TP9, TP10, P9, P10, PO9, and PO10). These time segments were defined by the interval of ± 20 ms placed around the peak latency of the grand mean (defined at the electrode where the respective ERP component was maximal). Finally, late effects in the time interval of 400 to 600 ms were analysed using mean amplitudes in that interval at 9 electrodes (F3, F4, C3, C4, P3, P4, Fz, Cz, and Pz). Where appropriate, epsilon correc-

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[4] For the clearly pronounced P1 and N170 components all analyses were also performed on peak amplitudes. For P1, individual peak amplitudes were measured at electrodes O1 and O2 as largest positivities in the time window of 90 – 130 ms. For N170, peak amplitudes were individually determined for each participant and hemisphere as amplitudes at the latency of the maximal negative peak between 150 – 200 ms within electrodes P7, P9, PO9, and TP9 as well as P8, P10, PO10, and TP10. If not otherwise stated, these analyses led to the same effects as those on mean amplitudes reported here.

tions for heterogeneity of covariances were performed (Huynh & Feldt, 1976). All post-hoc *t* tests were corrected according to the Bonferroni-procedure (α = .05).

Please note that in analogy to and for an easier comparison with the gender adaptation study by Kovács et al. (2006) the morphlevel of test faces has not been included as a factor in the analysis of the ERP data.

P1

The analysis of P1 amplitudes in a repeated-measurements ANOVA with the factors Electrode (O1/O2, P9/P10, PO9/PO10, and TP9/TP10), Hemisphere (left, right), Modality of adaptor (visual, acoustic), and Gender of adaptor (androgynous, male) revealed significant main effects of electrode (*F*[3, 54] = 58.19, *p* < .001), and modality (*F*[1, 18] = 78.91, *p* < .001), and significant two-way interactions of Electrode and Modality (*F*[3, 54] = 24.65, *p* < .001) and Modality and Gender (*F*[1, 18] = 15.52, *p* < .01). Post-hoc *t* tests revealed that the interaction between Electrode and Modality resulted from significantly smaller P1 amplitudes in trials following acoustic as compared to visual adaptation at electrode sites O1/O2 (*t*[18] = -7.08, *p* < .001), P9/P10 (*t*[18] = -7.01, *p* < .001), and PO9/PO10 (*t*[18] = -7.19, *p* < .001), but not at TP9/TP10 (*p* > .60). The interaction of the factors Modality and Gender resulted from the fact that test faces following face adaptation trials were characterised by significantly larger amplitudes in trials following adaptation to androgynous gender (M = 3.19 µV) than following adaptation to male gender (*M* = 2.95 µV, *t*[18] = 3.69, *p* < .01). For test faces following voice adaptation trials, however, the pattern was reversed. Here, test faces evoked significantly smaller amplitudes if presented following adaptation to androgynous (*M* = 1.45 µV) as compared to male gender (*M* = 1.67 µV, *t*[18] = -2.89, *p* < .05).

The analysis of P1 peak latencies in a 2 x 2 x 2 – ANOVA with Hemisphere, Modality of adaptor, and Gender of adaptation stimulus revealed a significant main effect of modality (*F*[1, 18] = 13.81, *p* < .01) reflecting significantly later P1 peaks in trials following face adaptation (*M* = 118.5 ms) than in trials following voice adaptation (*M* = 113.6 ms).

N170

N170 amplitudes were analysed in a repeated measurements ANOVA with Electrode (P7/P8, P9/P10, PO9/PO10, and TP9/TP10), Hemisphere (left, right), Modality of adaptor (visual, acoustic), and Gender of adaptor (androgynous, male) as factors. The analysis revealed a significant main effect of electrode (*F*[3, 54] = 8.03, *p* < .01), a main effect of hemisphere (*F*[1,18] = 5.60, *p* < .05), a main effect of modality (*F*[1, 18] = 114.96, *p* < .001), significant two-way interactions of the factors Electrode and Modality (*F*[3, 54] = 11.89, *p* < .001), Hemisphere and Modality (*F*[1, 18] = 13.01, *p* < .01), Hemisphere and Gender (*F*[1, 18] = 5.47, *p* < .05), and a three-way interaction of Electrode, Hemisphere, and Gender (*F*[3, 54] = 4.54, *p* < .01). The main effect of modality reflects substantially larger N170 amplitudes in response to test faces preceded by voice adaptors (*M* = -3.86 μV) as compared to face adaptors (*M* = -1.78 μV, see Figure 26).

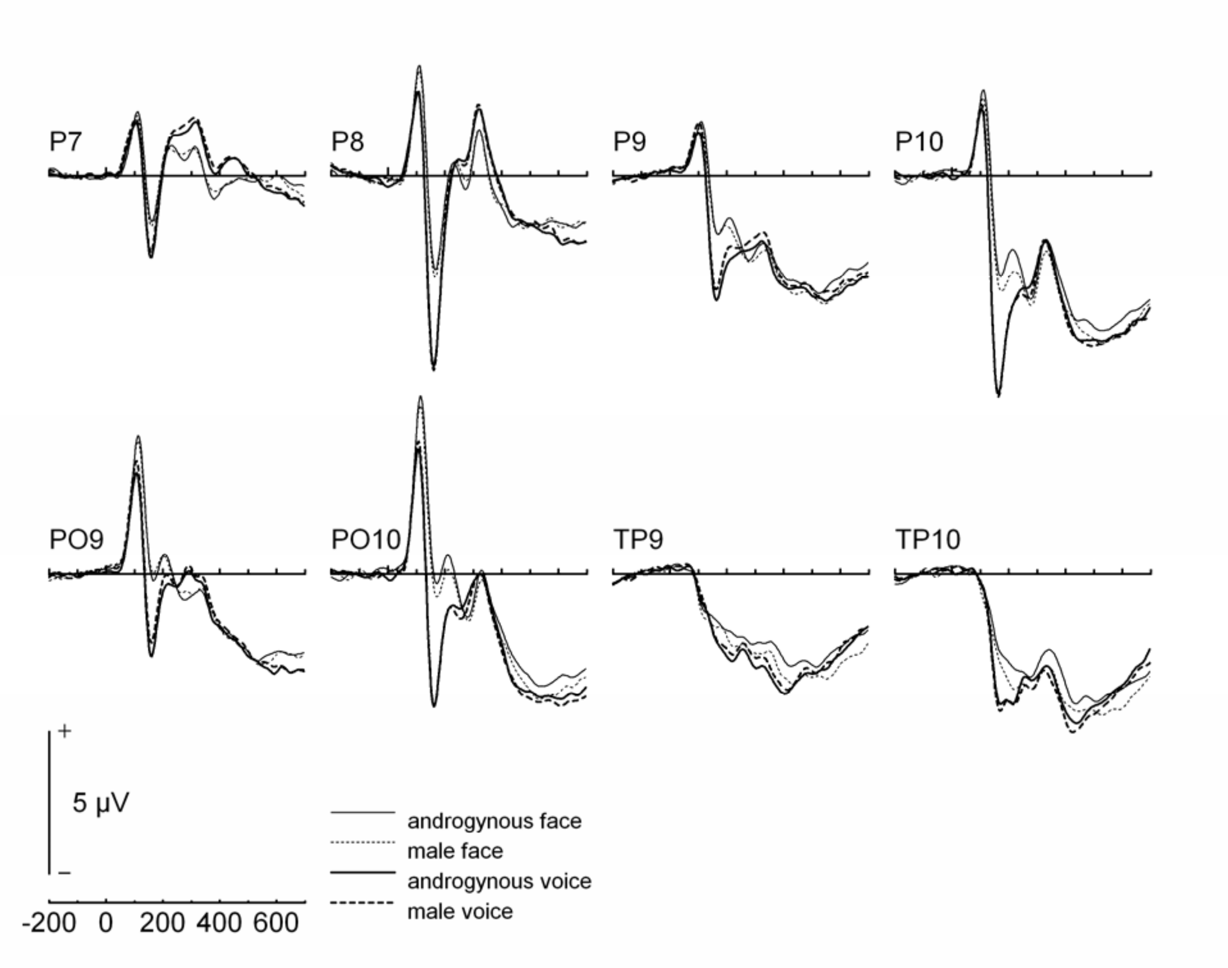

Figure 26: ERPs to test faces either preceded by adaptor faces (thin lines) or voices (bold lines) of androgynous (solid lines) or male gender (dashed lines).

Though measurable at each of the electrode locations, the modality effect was more pronounced at electrode sites P7/P8, P9/P10, and PO9/PO10 than at TP9/TP10 and was more distinct over right (*M* = -2.40 μV, *M* = -5.20 μV, for mean amplitudes after visual and acoustic adaptation, respectively) than left hemispheric sensors (*M* = -1.17 μV, *M* = -2.52 μV for mean amplitudes after visual and acoustic adaptation, respectively).

The comparison of the differences obtained for the left and right hemisphere reached statistical significance (*t*[18] = 3.61, *p* < .01). The three-way interaction between Electrode, Hemisphere, and Gender was further analysed in separate analyses for each electrode with Gender as a factor. The analyses revealed a significant main effect of gender only for electrode location PO9 (*F*[1, 18] = 5.32, *p* < .05) due to smaller (i.e. less negative) amplitudes after male adaptation (*M* = -0.72 μV) as compared to androgynous adaptation (*M* = -1.06 μV).

The analogous analysis of *peak amplitudes* mainly replicated the above findings. However, there was also an additional four-way interaction of Electrode, Hemisphere, Modality, and Gender (*F*[3, 54] = 3.60, *p* < .05) reflecting that, in addition to the main effect of gender at electrode PO9 (*F*[1, 18] = 23.62, *p* < .001) due to the smaller N170 amplitudes following male adaptation (M = -1.79 μV) than androgynous adaptation (*M* = -2.17 μV), there was also a significant main effect of gender at electrode PO10 (*F*[1, 18] = 4.50, *p* < .05) due to significantly larger N170 amplitudes following male (*M* = -4.07 μV) than androgynous adaptation (*M* = -3.78 μV). For an overview of the gender effects, please see Figure 27.

The analysis of N170 peak latencies in a 4 x 2 x 2 x 2 – ANOVA with Electrode, Hemisphere, Modality, and Gender as factors revealed a main effect of modality (*F*[1, 18] = 10.87, *p* < .01) reflecting significantly longer N170 latencies in trials following face adaptation (*M* = 165.1 ms) than in trials following voice adaptation (*M* = 161.9 ms, see Figure 26).

P2

The analysis of P2 amplitudes in a 4 x 2 x 2 x 2 – ANOVA with Electrode, Hemisphere, Modality, and Gender as factors revealed significant main effects of electrode (*F*[3, 54] = 30.10, *p* < .001), hemisphere (*F*[1, 18] = 4.53, *p* < .05), and modality (*F*[1, 18] = 8.88, *p* < .01). Further, there was a significant interaction between the factors Electrode and Modality (*F*[3, 54] = 6.30, *p* < .01) reflecting that the modality effects with more positive P2 amplitudes following face as compared to voice adaptation were restricted to electrode locations P9/P10, PO9/PO10, and TP9/TP10, but did not reach significance for electrode location P7/P8 (see Figure 26 and Table 6).

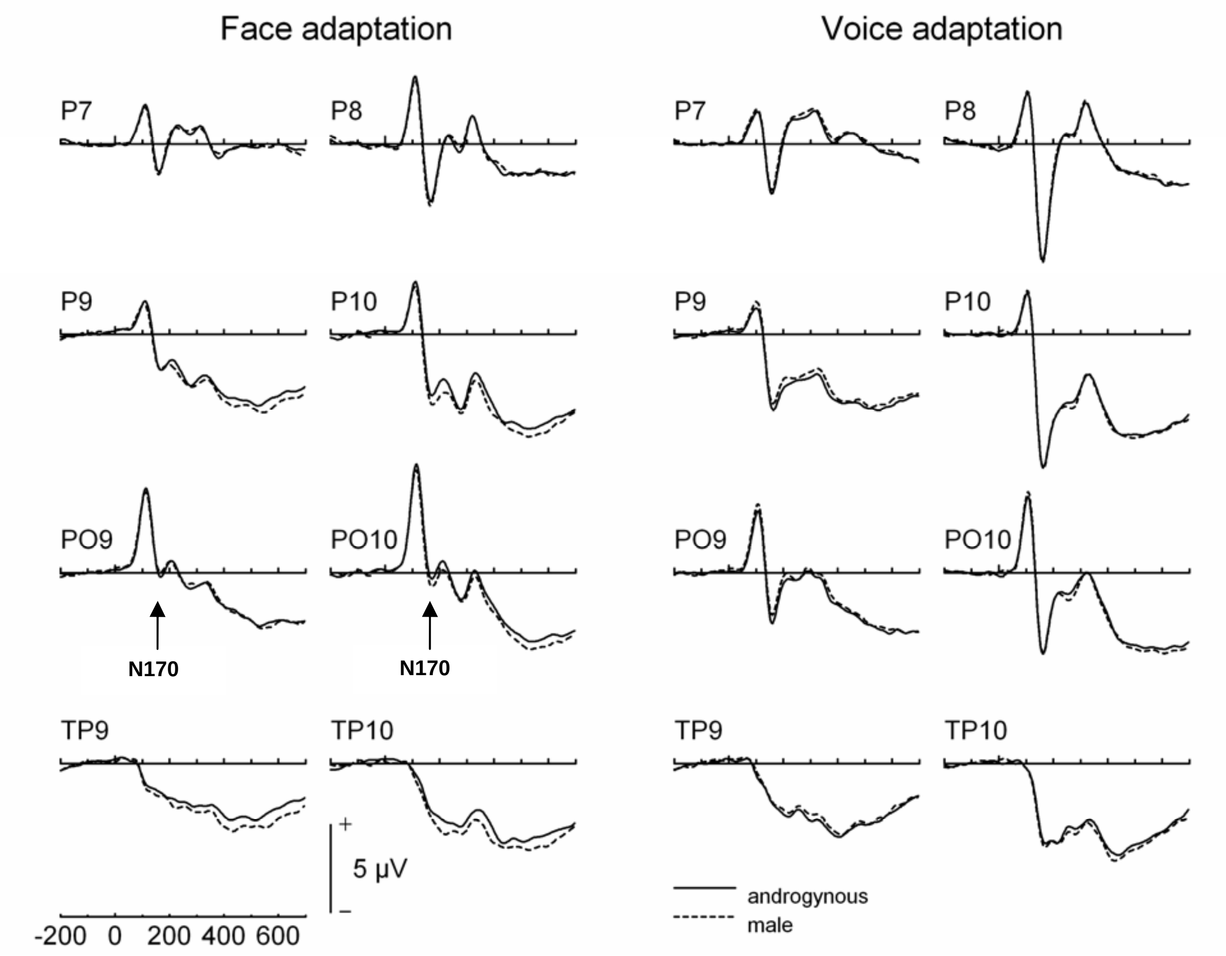

Figure 27: Left column: ERPs to test faces presented after adaptation to *faces* of androgynous (solid lines) or male (dashed lines) gender. Please note the small but significant differences in N170 amplitudes evoked by androgynous and male face adaptation at electrodes PO9 and PO10 as indicated by the arrows. Right column: ERPs to test faces presented after adaptation to *voices* of androgynous (solid lines) or male (dashed lines) gender.

	Paired differences					
Pair	*M*	*SD*	*SEM*	*T*	*df*	*p*
P7/P8: FaceA – VoiceA	0.23	1.33	0.30	0.74	18	0.466
P9/P10: FaceA – VoiceA	1.32	1.76	0.40	3.27	18	0.004
PO9/PO10: FaceA – VoiceA	0.78	1.07	0.25	3.17	18	0.005
TP9/TP10: FaceA – VoiceA	1.24	1.76	0.40	3.08	18	0.006

Table 6: Results of *t* tests separately analysing the existence of modality effects for each of the homologue electrode pairings.

Late positive component

ERPs to test faces in the time range of 400 - 600 ms at electrode locations F3, F4, C3, C4, P3, P4, Fz, Cz, and Pz (see Figures 28 and 29) were analysed in a repeated measurements ANOVA with Electrode location (frontal, central, parietal), Hemisphere (left, middle, right), Modality of adaptor (visual, acoustic), and Gender of adaptor (androgynous, male) as factors. This analysis revealed significant main effects of electrode location (*F*[2, 36] = 75.45, *p* < .001), hemisphere (*F*[2, 36] = 16.31, *p* < .001), a significant two-way interaction between Electrode location and Hemisphere (*F*[4, 72] = 17.81, *p* < .001), and a significant three-way interaction between Electrode location, Modality, and Gender (*F*[2, 36] = 3.91, *p* < .05). To analyse the three-way interaction, separate analyses were conducted for the groups of frontal, middle, and parietal electrodes, respectively. They revealed a significant interaction of Modality and Gender for parietal electrodes (*F*[1, 18] = 5.00, *p* < .05) and a strong trend for central electrodes (*F*[1, 18] = 4.21, *p* = .05). *T* tests revealed that these interactions were due to significantly larger, i.e. more positive amplitudes following male face than androgynous face adaptation (*t*[18] = 2.41, *p* < .05, *t*[18] = 2.33, *p* < .05, for central and parietal electrodes, respectively, see Figure 28). No such effects of adaptor gender were found in trials following voice adaptation (all *p*s > .40, see Figure 29).

The differences observed in the late positive component might be explained in terms of a P3 effect with larger amplitudes arising in response to deviating stimuli. Considering the design of the experiment, both androgynous and male face adaptors were followed by an equal set of test stimuli consisting of relatively feminine faces (20% male/80% female), of gender-ambiguous faces (40% /60% and 60% male/40% female), and of relatively masculine faces (80% male/20 % female). Consequently, there was a varying overall rate of deviance between androgynous and male adaptation trials, i.e. the total dissimilarity of test stimuli from the adaptor stimuli was different for the two adaptation conditions. More precisely, in the androgynous adaptation condition, 50% of the tests faces contained similar androgynous gender information (i.e. 40%/60% and 60% male/40% female) as the adaptor faces (50% male/50% female) and the resulting 50% of test faces (i.e. the relatively male and relatively female faces) were dissimilar yet relatively close with regard to their gender information: they deviated to the same extent although in a different direction from the androgynous faces, which lay halfway between male and female faces.

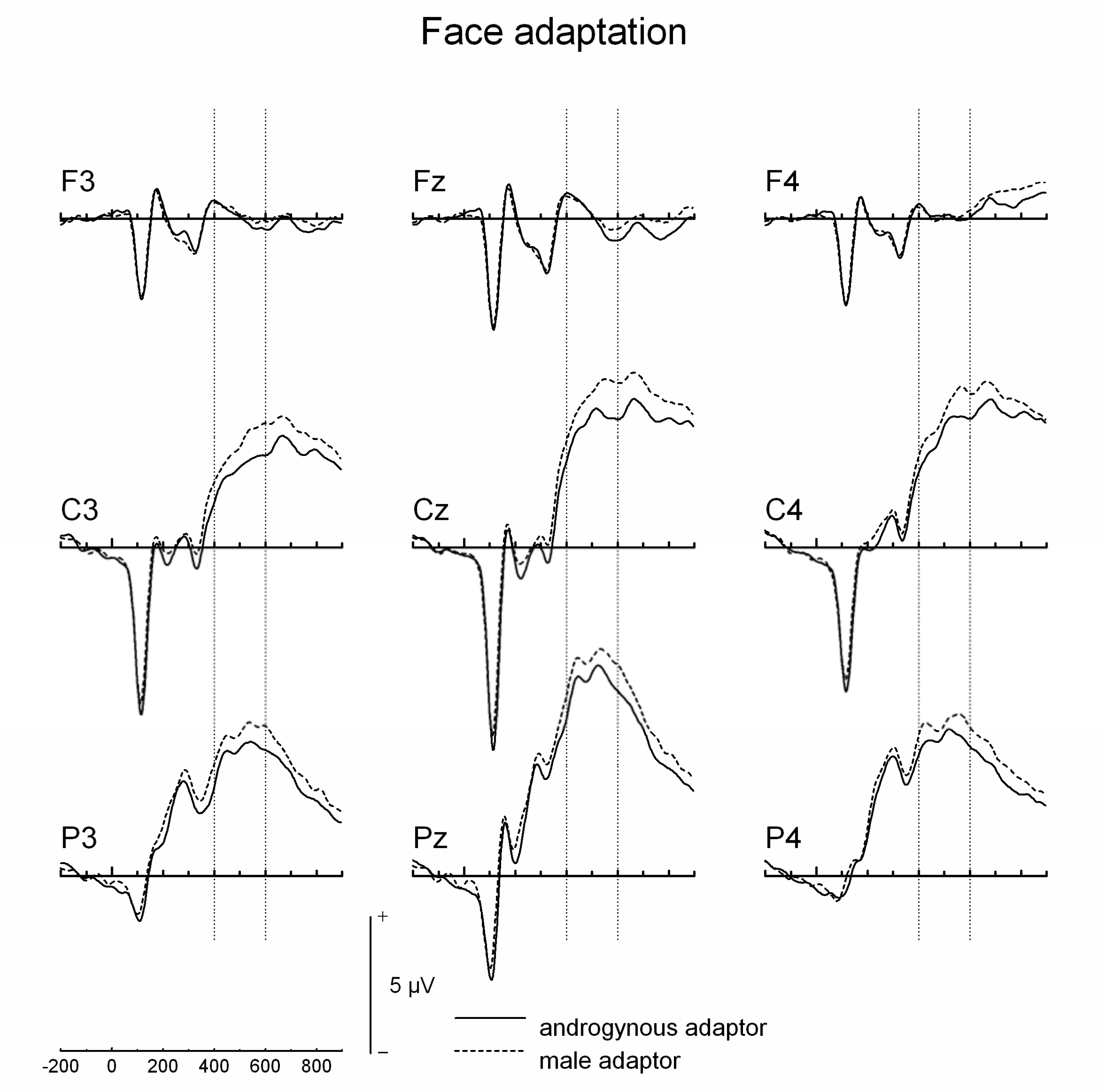

Figure 28: Effects of adaptation to facial gender in the time interval between 400 and 600 ms (vertical lines). ERPs in response to test faces presented following androgynous (solid lines) or male (dashed lines) face gender adaptation, respectively. Please note the larger amplitudes in trials following adaptation to male as compared to androgynous gender at central and parietal electrodes.

In the male adaptation condition, however, only 25% of the test faces (i.e. 80%male/ 20% female) contained similar gender information as the adaptor stimuli. The 50% of test faces showing ambiguous test stimuli contained dissimilar yet relatively close gender information, whereas the 25% of test faces that contained relatively feminine information (i.e. 20% male/ 80% female) were very dissimilar to the male adaptation stimuli.

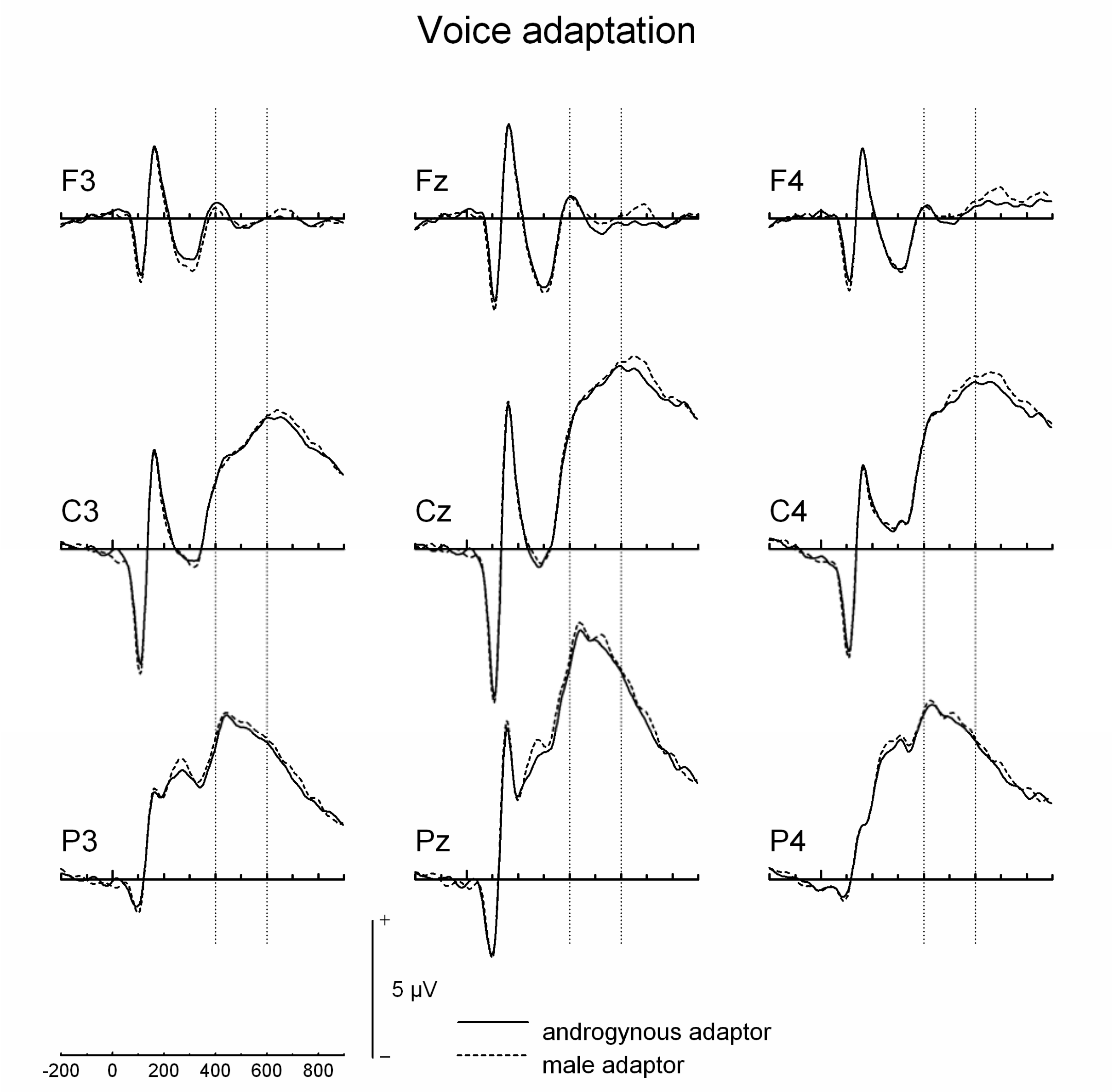

Figure 29: Effects of adaptation to voice gender in the time interval between 400 and 600 ms (vertical lines). ERPs in response to test faces presented following androgynous (solid lines) or male (dashed lines) voice gender adaptation, respectively. Please note the absence of effects of adaptor gender which were very prominent in face adaptation conditions (cf. Figure 28)

Considering the relationship between adaptation and test stimuli in this way, i.e. in terms of the total amount of deviance of gender information in test stimuli from the gender information in adaptation stimuli, the sum of test faces in the male face adaptation condition contained more gender deviance than did the total amount of test faces in the androgynous face adaptation condition. This might explain the larger positivity between 400 and 600 ms evoked by test stimuli following male as compared to androgynous adaptation.

Further analyses were conducted to test this possible explanation of the effects in the time interval of 400 to 600 ms. The rationale behind these analyses was the following: if the observed effects should represent a P3 effect with more positive amplitudes in response to stimuli deviating from the context given by adaptor faces, this effect should be largest for relatively female faces with more positive amplitudes following male than androgynous adaptation for test stimuli of the morphlevel 20% male/80% female. Further, decreasing effects might be predicted for morphlevels with increasing proportions of maleness. Figure 30 separately depicts the effects in the interval of 400 to 600 ms for the four different morphlevels used.

In order to evaluate the statistical significance of amplitude differences observed in the late time interval for test stimuli of the different morph levels a repeated measurements ANOVA was conducted on mean amplitudes obtained between 400 and 600 ms. The ANOVA investigated the effects of Electrode location (C3, Cz, C4, P3, Pz, and P4), Gender of the adaptor (androgynous, male), and the Morphlevel of the test stimulus (20%/80%, 40%/60%, 60%/40%, and 80% male/20% female ratio). The analysis revealed significant main effects of electrode (*F*[5, 90] = 35.61, *p* < .001), gender (*F*[1, 18] = 5.04, *p* < .05), and morphlevel (*F*[3, 54] = 6.58, *p* < .05), as well as a significant interaction of Gender and Morphlevel (*F*[3, 54] = 4.99, *p* < .01). *T* tests revealed that only the relatively feminine stimuli, i.e. test stimuli of the morphlevel 20% male/80% female produced significantly larger positivity following male than androgynous face adaptation (*t*[18] = 3.84, *p* < .01) whereas for all other morphlevels amplitudes evoked between 400 – 600 ms did not significantly differ between androgynous and male adapted trials (all *p*s > .10).

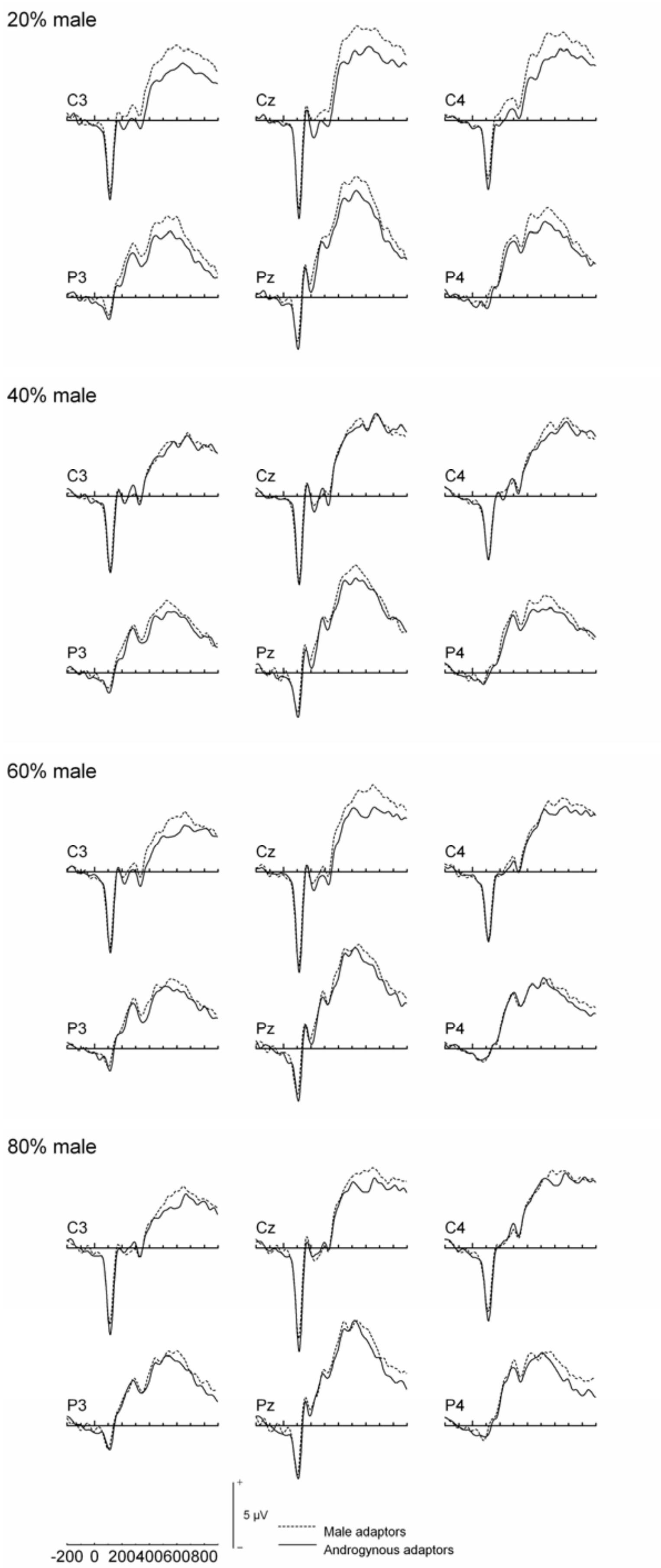

Figure 30: Effects of adaptor gender on test faces of the different morphlevels in the time interval of 400 to 600 ms.

6.4 Discussion

The adaptation procedure applied in Experiment 4 evoked clear and significant effects of adaptation to gender. As has been shown before, adaptation to male faces led to an increase in female classifications of subsequently presented face stimuli with relatively high gender-ambiguity. Interestingly, a similar shift in the perception of facial gender did also seem to take place following adaptation to male voices. Although the significance of this cross-modal gender adaptation effect could not be proven in all analyses, there is still some statistical support for the assumption that the perception of gender in faces can be biased by the preceding voice information. This is the first evidence for cross-modal adaptation effects. Whereas Kovács et al. (2006) have shown that the perception of gender in hands is generally vulnerable to adaptation effects in an intra-category adaptation condition, the perception of gender in faces was found to be unaffected by previous presentation of hand adaptors. Considered together, these findings suggest that the perception of gender in faces is unaffected by cross-category adaptation whereas some cross-modal adaptation seems to occur following the presentation of voices.

The frequent co-occurrence of faces and voices in everyday life compared to relatively few cases of simultaneous presentation of faces and hands might explain for the different findings on cross-category gender adaptation. Additionally, considering that much of our communication takes place over the phone and therefore only provides acoustic information, it is likely that we are very experienced in extracting gender information from voices. However, when deciding about the gender of a person in a direct personal interaction, we usually make this decision on the basis of the persons' face rather than his or her hands. The current finding of cross-modal adaptation to gender might therefore be explained in terms of adaptation to a superordinate, high-level, and modality-invariant gender concept that subsumes different kinds of sensory information, such as visual, acoustic, and olfactory information. This hypothesis is in line with a study by Kovács et al. (2004) describing influences of sex-hormone-like odours on the perception of gender-ambiguous faces.

However, given the relatively small statistical support for cross-modal gender adaptation that certainly suggests the effect to be rather weak and considering that a recent study investigating voice adaptation did not observe an effect of face adaptation on the gender classification of ambiguous voices (Schweinberger et al., 2008) the present findings have to be considered with caution. It is evident that further research will be needed to shed light on the complex multimodal aspects of gender perception. Of special importance, the cross-modal voice-to-face gender adaptation effect described here will have to be replicated. The inconsistent results in the different statistical analyses suggest that cross-modal adaptation effects have a relatively large variance. Further, the cross modal effect appears to be somewhat weaker than the unimodal adaptation effect. Finally, it might even be the case that different individual predispositions (e.g. sharp vs. poor sense of hearing) lead to interindividual differences with regard to the emergence and magnitude of cross-modal adaptation effects. These considerations might be accounted for in studies trying to replicate the present results with a larger number of participants and trials.

The major findings concerning the ERP correlates of this study were as follows. The N170 was shown to be mainly sensitive to adaptor modality, with test faces evoking dramatically larger N170 amplitudes when presented after voice adaptors than after face adaptors. Relative to that great effect, only a relatively small effect of adaptor gender was found in the N170 measured at electrode pair PO9/PO10 due to slightly smaller amplitudes following male as compared to androgynous adaptation at electrode PO9 and a reversed pattern with significantly larger amplitudes following male than androgynous adaptation at electrode PO10.

The effects observed in the N170 are largely in line with the hypotheses of this study and underline the methodical considerations following Experiment 1: the large reduction in N170 amplitudes following adaptation to male gender as observed by Kovács et al. (2006) seems to consist of both a large general face adaptation effect and a relatively small contribution of a gender specific face adaptation effect. The size of the amplitude reduction observed by Kovács et al. (2006) which was in the range of ~3 µV is at a similar scale as the modality effect observed in the current experiment. The gender effects observed, however, were relatively small and limited to the occipitotemporal electrodes PO9 and PO10. Interestingly, the N170 gender adaptation effect interacted with the factor hemisphere with adaptation to male gender (as compared to androgynous gender) evoking significantly smaller amplitudes over the left hemisphere and significantly larger amplitudes over the right hemisphere. While there is no clear interpretation of these results at present, they can be reconciled with a recent study by Parente and Tommasi (2008) suggesting some degree of laterality in the processing of facial gender as will be discussed in more detail in the general discussion of this thesis. However, it is important to consider that this effect is relatively small and requires replication in order to base possible interpretations on the functional relevance of this effect on more established findings.

More pronounced effects of gender adaptation could be observed in the late positive component over central and parietal electrode locations. Here, test faces elicited more positive amplitudes following adaptation to male as compared to androgynous faces. Although a small numerical effect in this direction was also found for test stimuli preceded by voice adaptors, this was far from reaching statistical significance.

Further analyses considering the different morph levels of the test stimuli aimed at a deeper understanding of the nature of this late effect. In line with the assumption of a P3 effect, amplitude differences between male adapted and androgynous adapted trials were largest for relatively female test stimuli, with more positive amplitudes following male as compared to androgynous adaptation. This finding is in line with the ‘context-updating theory’ of the P3 (Donchin, 1981) that assumes larger P3 amplitudes to reflect the larger effort of context updating for stimuli that differ from the previous perceptual context. In the current experiment, the largest perceptual difference between adaptation and test stimuli existed between male adaptation stimuli and relatively feminine (80% female) test stimuli. All other stimulus combinations were perceptually more similar and did not evoke significant differences in P3 amplitudes. Importantly, this explanation does also account for the fact that there were no effects in the late positive components evoked by test faces in voice adaptation trials. Here, the preceding stimulus context was given by a completely different modality therefore possibly requiring a similar context updating effort for all different kinds of test stimuli.

7. General Discussion

In a series of four studies the current work investigated the nature of high-level adaptation effects in the perception of faces. Experiments 1, 2, and 3 investigated the effects of adaptation to eye gaze direction with different degrees of deviance from direct gaze and examined the neural correlates and the time-course of gaze adaptation effects, respectively.

Experiment 4 examined the neural correlates of gender adaptation in intra- and inter-modality adaptation trials. For this purpose, a new control adaptation condition has been applied which was developed as a consequence of the findings of Experiments 1 and 2.

7.1 Behavioural findings on eye gaze adaptation

Although Experiments 1, 2, and 3 all investigated effects of adaptation to eye gaze, they used different experimental parameters allowing broad insight into the conditions under which gaze adaptation occurs. Effects of adaptation to right gaze direction could be observed both in the case of adaptation to faces with large gaze deviations from direct gaze (25°, Experiments 1 and 3) and in the case of adaptation to faces with smaller gaze deviations (10°, Experiment 2) leading to a misperception of eye gaze deviating in the adapted direction as gazing directly at the observer. The results of Experiments 1, 2, and 3 were therefore able to replicate the gaze adaptation effects that have been reported in earlier studies (Jenkins et al., 2006; Seyama & Nagayama, 2006). Additionally, they provided further information on the nature of gaze adaptation effects in examining the neural correlates (Experiments 1 and 2) and the temporal persistence of these effects (Experiment 3).

Experiment 2 provided new information on the interrelation of the nature of adaptation and test stimuli and their ability to evoke gaze aftereffects. Considering that the gaze deviations of adaptor stimuli in former studies showed substantial 25° (Jenkins et al., 2006, Experiment 1 of the present thesis) or 35° deviations from direct gaze (Seyama & Nagayama, 2006) and were very dissimilar to the test stimuli used (5° and 10°, 2° and 4°, respectively), this study has provided the first evidence that adaptation to eye gaze direction can be elicited by stimuli with substantially smaller (10°) deviations from direct gaze. The size of aftereffects on test stimuli with 5° gaze deviance in the adapted direction was found to be smaller when elicited by adaptation stimuli with 10° deviance (Experiment 2) as compared to adaptation stimuli with 25° deviance in the right direction (Experiments 1 and 3). The number of incorrect “direct” classifications increased from approximately 30% in the baseline condition to about 60% following adaptation to 10° right gaze. Following adaptation to 25° right gaze it increased from approximately 30% in the baseline condition to about 90%, therefore closely replicating the magnitude of the gaze adaptation effect reported by Jenkins et al. (2006). Moreover, Experiment 2 showed that adaptation to a small degree of gaze deviation even has small but significant effects on the perception of test stimuli with the same 10° gaze deviation as contained in the adaptation stimuli. Here, the number of incorrect “direct” classifications significantly increased from about 6% in the baseline condition to approximately 13% following adaptation. Overall, these findings are in line with the suggestion by Robbins et al. (2007) who proposed that those facial characteristics for which a large range of values has to be coded evoke aftereffects that increase when the adaptation stimulus is shifted away from the norm. For different facial attributes that only vary in a relatively small range, Robbins et al. (2007) claimed that aftereffects decrease the further the adaptation stimulus is placed away from the norm.

The comparison of a new direct gaze adaptation control condition to the traditional pre-adaptation condition which had been used by Jenkins et al. (2006) and in Experiment 1 revealed that adaptation to direct gaze did not have an effect on the perception of subsequently presented gaze directions. Rather, it led to the same classifications of gaze direction as obtained without any adaptation procedure. This finding suggests that direct eye gaze serves as a neutral point in the representation of gaze directions

Along with the theoretical implication of considering direct gaze as a neutral point in the neural representation of gaze directions, the comparison of the pre-adaptation and direct gaze adaptation conditions also suggested that adaptation to direct gaze can indeed be considered as an adaptation-neutral condition. This condition therefore met the requirements for serving as a suitable new control condition for ERP studies: although presenting the same amount of facial information before each test stimulus as displayed in the directional adaptation condition, direct gaze adaptation did not produce adaptation effects in itself.

A few adaptation studies have begun to address the question of contrastive (two-pool) vs. multichannel coding of faces. These neural coding models have traditionally been investigated using adaptation paradigms in low-level vision (Clifford, Wenderoth, & Spehar, 2000; Rogers & Graham, 1985) and have recently also been applied to studies on high-level aftereffects (Robbins et al., 2007). Two-pool models have usually been considered appropriate for the perception of dimensions which contain a neutral point. These models assume a contrastive processing where opposite characteristics of a stimulus dimension are coded by different neural entities, and a neutral point between those characteristics is perceived when activity in the two neural pools is at an equilibrium (e.g. the perception of vertical motion with standstill as the neutral point between upward motion and downward motion). In the case of eye gaze direction perception, a two-pool model would assume that one neural entity selectively processes left gaze direction and a second neural entity selectively processes right gaze direction. Direct gaze direction would be assumed to be perceived as a consequence of equal activity in both pools.

Multichannel models, however, may be applicable for the processing of dimensions that do not have a neutral point (e.g. spatial frequency). They propose the existence of several channels with each of them coding a certain range within the dimension of a certain stimulus attribute. The minimal account of a multichannel system applied to the perception of eye gaze direction would assume three different channels – one for the perception of left, direct, and right gaze direction, respectively – whereas a more refined multichannel system might also code different gaze deviations, e.g. 30° left, 20° left, 10° left, 0° (i.e. direct gaze), 10° right, and so on.

Concerning the application of these models on the perception of different facial aspects as investigated in high-level visual aftereffects, most authors have reported evidence for contrastive coding in studies investigating for example identity adaptation (see Leopold et al., 2001, for a study strongly suggesting that identity is coded relative to an average face) or adaptation to symmetrical and asymmetrical face distortions (see Robbins et al., 2007). Jenkins et al. (2006) stated that their findings on eye gaze adaptation would be both in line with a two-channel and a multichannel coding mechanism and concluded that further research would be required to come to a decision about the nature of eye gaze representations.

The behavioural results obtained in the Experiments 1, 2, and 3 of the present thesis might well be reconciled with the idea of contrastive (two-channel) coding of horizontal eye gaze direction. Although it is difficult to completely exclude a multichannel system with separate channels for distinct gaze directions on the basis of the present data, at least when assuming relatively broad tuning curves of individual channels, three aspects of the current data seem to be more in line with the idea of contrastive coding of gaze direction: first, multichannel models predict adaptation effects to mainly arise for test stimuli close to the adaptor (Robbins et al., 2007). The data of Experiments 1 and 3, however, showed that adaptation to eye gaze deviating by 25° caused substantial and more persistent aftereffects for the perception of 5° test stimuli as compared to 10° test stimuli. Moreover, the behavioural data of Experiment 2 clearly showed that aftereffects on stimuli identical to the adaptor were significantly weaker than those on stimuli that were dissimilar to the adaptor, but more ambiguous. Second, unlike the basic results of Jenkins et al. (2006), but similar to the findings of Seyama and Nagayama (2006), adaptation to right gaze consistently not only impaired the observer's perception of gaze in the adapted direction, but also improved the observer's perception of gaze in the opposite direction, again supporting the idea that adaptation effects to eye gaze reflect the coding of gaze direction in a contrastive manner. Third, the comparison of gaze classifications obtained in a traditional pre-adaptation baseline to those acquired in a direct gaze adaptation baseline in Experiment 2 suggested that adaptation to direct gaze did not lead to a bias in the perception of gaze direction, again suggesting direct gaze to be represented as the neutral point between left and right gaze direction.

In a very recent study, Calder et al. (2008) systematically examined the nature of eye gaze representations using adaptation paradigms to test different predictions derived from the two models. First, they investigated the effects of adaptation to direct eye gaze. According to the authors, adaptation to direct gaze if represented in a multichannel system should lead to an attenuation of the channel representing direct gaze and lead to the perception of small gaze deviations as being more averted. In an opponent channel system, however, they claimed that adaptation to direct gaze should lead to an equivalent attenuation of channels coding left and right gaze direction, which should not lead to a change of any perceived gaze direction. Second, Calder et al. (2008) stated that the two models make different predictions for the effects of adaptation to different degrees of gaze deviation (10° and 25°), with a multichannel model predicting that adaptation to 25° stimuli should lead to a larger probability of perceiving gaze stimuli averted in the adapted side as showing direct gaze relative to the 10° adaptation condition. Further, they expected adaptation to 10° gaze represented in a multichannel model to lead to a decreased tendency to perceive gaze directed to the unadapted side as direct relative to the 25° adaptation condition. They stated that these effects result from a larger attenuation of the direct gaze channel by 10° than 25° adaptors. According to Calder et al. (2008), however, a two-channel model allows for two possible outcomes when comparing adaptation to different degrees of gaze deviation (i.e. 10° and 25°): first, it is possible that adaptation to 25° would both increase the probability of “direct” responses to stimuli gazing to the adapted side and decrease the probability of “direct” responses to stimuli gazing to the unadapted side to a greater extent than adaptation to 10°. As a second prediction in line with the two-channel model, they stated that both adaptor types (10° and 25°) might lead to equivalent effects on test stimuli with gaze directed to the adapted and unadapted sides. Calder et al. (2008) derived these two possible predictions from the consideration that the shift in the central tendency due to adaptation is proportional to the degree of attenuation of the left or right channel, so that adaptation to 25° gaze deviance might be assumed to produce either an equal or more pronounced attenuation of the adapted channel than adaptation to 10° gaze deviance.

Testing these different predictions, Calder et al. (2008) conducted two studies and investigated (a) the effects of adaptation to left (25° and 10°), right (25° and 10°), and direct gaze direction on the perception of test stimuli (10° left, 5° left, direct, 5° right, and 10° right) and (b) the effects of simultaneous adaptation to alternating presentations of 25° left and 25° right gaze, leading to equivalent habituation of both left and right channels.

The main results were as follows: adaptation to direct gaze was found to significantly decrease the number of “direct” responses to test stimuli gazing 5° in both the left and right direction and, to a lesser extent, to test stimuli gazing 10° in both the left and right direction. Comparing adaptation to 25° and 10°, the former led to a larger increase in incorrect “direct” classifications of gaze to the adapted direction compared to the 10° adaptation stimuli, whereas the 10° adaptors led to a reduced tendency to perceive eye gaze to the unadapted side as direct. Finally, they showed that after simultaneous adaptation to faces with alternating left and right gaze directions participants made significantly more “direct” judgements to both 5° and 10° left and right test faces. These findings are in strong contradiction to a two-channel coding of gaze direction, whereas they can be well explained by the multichannel assumption. Based on this series of findings, the authors therefore suggested that eye gaze direction is coded in a multichannel system

Although the studies on eye gaze adaptation presented in the current thesis were designed to investigate neural correlates of gaze adaptation (Experiments 1 and 2) and the temporal decay of that effect (Experiment 3) and did not systematically investigate the question of two-channel versus multichannel coding, part of their findings clearly contradict the results of Calder et al. (2008). Whereas the finding that adaptation to faces with larger gaze deviations (i.e. 25°) induced stronger aftereffects than adaptation to smaller gaze deviations (i.e. 10°) could also be observed in the comparison of Experiments 1 and 2, there were large differences in the findings concerning the effects of adaptation to direct gaze direction. Calder et al. (2008) reported that adaptation to direct gaze significantly decreased the number of “direct” responses to test stimuli gazing 5° in both the left and right direction and, to a lesser extent, to test stimuli gazing 10° in both the left and right direction. In Experiment 2 of the present thesis, however, the comparison of behavioural effects of adaptation to direct gaze to those obtained in a traditional pre-adaptation phase without adaptation revealed no differences between the conditions, suggesting no effect of adaptation to direct gaze whatsoever. This is clearly in line with a two-pool model account on gaze perception expecting both channels coding left and right gaze direction to equally adapt when presented with direct gaze, therefore not leading to a disproportionate habituation of any channel which would result in behavioural aftereffects.

Overall, the contradictory results observed following direct gaze adaptation underline that the nature of the neural coding of gaze directions is still not completely discovered. Whereas some aspects seem to be consistently found in different studies, such as larger adaptation effects following adaptation to large as compared to small gaze deviations, other findings are difficult to integrate: the fact that adaptation to direct gaze did not influence the perception of subsequently presented test stimuli in Experiment 2 is a serious challenge for the assumption that eye gaze is coded in a multichannel system. Further research will be required to understand the origin of these conflicting findings.

7.2 ERP correlates of eye gaze adaptation

In the analysis of the ERP data collected in Experiments 1 and 2, two time windows consistently emerged as being of relevance for eye gaze adaptation: the occipitotemporal N170 component and the time interval of 250 – 350 ms. In Experiment 1, the N170 was largely affected by adaptation irrespective of the direction of gaze, with a substantial reduction in amplitude and an increase in latency in post-adaptation trials as compared to the pre-adaptation baseline. Due to the direction-invariance of this effect it was hypothesised to merely reflect a correlate of general face adaptation irrespective of the eye gaze direction. As a result of the design of pre-adaptation and post-adaptation trials in the study, test faces presented in post adaptation trials were always closely preceded by top-up adaptation displays. These trials therefore provided a higher frequency of face repetitions than pre-adaptation trials, which were characterised by longer blank screen intervals between the presentations of test faces.

In order to test the hypothesis of a general face adaptation mechanism underlying this N170 amplitude reduction and to test the applicability of a methodically modified adaptation design for ERP studies, Experiment 2 compared the effects of adaptation to direct gaze and right gaze direction, therefore providing the same amount of face information before each test face in both adaptation conditions. This change of the design led to a completely different pattern of results in the N170 time window in which the large (~2 µV) N170 amplitude differences observed in Experiment 1 almost completely vanished. In line with this finding, the comparison of N170 amplitudes in response to the presentation of adaptation stimuli revealed significantly larger amplitudes in response to stimuli presented in the first halves of the adaptation blocks compared to the second halves. Again, these amplitude differences were independent of the direction of gaze contained in the adaptation stimuli, further stressing that the N170 is mainly sensitive to face repetitions in general.

Together, these findings suggest that the N170 effects observed in Experiment 1 indeed reflected adaptation to face stimuli per se, more precisely, they probably represented adaptation to their structural composition, the analysis of which is believed to be reflected in the N170 (Eimer, 1998; Eimer, 2000; Itier & Taylor, 2004a; Kanwisher & Moscovitch, 2000). This interpretation is in line with earlier studies that reported decreased amplitudes following face repetitions both in EEG (Itier & Taylor, 2002; Itier & Taylor, 2004b) and MEG studies (Harris & Nakayama, 2007; Jeffreys, 1996). The use of the new control condition of direct gaze adaptation therefore seemed to allow the disentangling of the relative contributions of general face repetition and gaze adaptation effects on the N170 and is therefore considered to be a promising new approach to study effects of adaptation in ERP studies.

The remaining N170 adaptation effects in response to test stimuli observed in Experiment 2 were very small: at P7/P8 a strong trend reflected larger amplitudes following right as compared to direct gaze adaptation. At PO9/10 the same pattern was found, but only for test stimuli showing left gaze direction which evoked larger N170 amplitudes following right as compared to direct adaptation. The fact that there were relatively small adaptation effects in the N170 time range in both Experiments 1 and 2 allows the exclusion of one possible explanation for finding no direction-specific effects in the N170 observed in Experiment 1. Considering that a possible N170 adaptation effect might have been covered by recovery from adaptation in Experiment 1, Experiment 2 investigated adaptation to stimuli with relatively small gaze deviations (10°) from direct gaze. This increased the perceptual similarity between adaptation and test stimuli and was therefore expected to decrease the amount of fast recovery of adaptation. The fact that N170 effects of adaptation were still very small in Experiment 2 therefore suggests that recovery of adaptation might not have played an important role with regard to the findings of Experiment 1.

To date, there is mixed evidence concerning the sensitivity of the N170 to gaze direction, with some studies observing sensitivity to gaze direction (Conty et al., 2007; Itier et al., 2007a; Puce et al., 2000; Watanabe et al., 2002) and other studies not finding it (Taylor et al., 2001). In the studies that reported effects of gaze directions averted eye gaze was usually found to elicit larger N170 amplitudes than direct gaze (but see Conty et al., 2007, for a report of larger N170 amplitudes in response to gaze movements from diverted to direct gaze as compared to movements from direct to averted gaze).

Visual inspection of the ERP responses to adaptation stimuli in Experiment 2 also revealed larger N170 amplitudes following right (i.e. averted) adaptation than direct adaptation, although these differences failed to reach statistical significance. It is important to note, however, that the small but significant effect found in the study, namely the finding of larger N170 amplitudes to left gazing test stimuli following right than direct adaptation is in line with the direction of amplitude differences reported by Itier et al. (2007) and Watanabe et al. (2002). Considering that adaptation to right gaze direction has been found to improve correct classifications of left gaze it is reasonable to assume that left gazing stimuli following right adaptation were more reliably perceived as averted. This finding might explain the increase in N170 amplitude following right adaptation: direct gaze was still perceived as direct in most cases after adaptation, possibly explaining why N170 amplitudes were found to be unaffected by adaptation. Following these considerations, right gaze direction, which was most often perceived as direct gaze (i.e. unaverted gaze) following adaptation, should have produced smaller N170 amplitudes as compared to the control condition. An effect in this direction, however, could not be observed.

The finding of only small effects in the N170 time window and the fact that the response to right gazing stimuli was not modulated in a way consistent with the explanation of the results for stimuli gazing in the left direction does not necessarily mean that the processes taking place in the N170 time window were not influenced by adaptation. It is possible that there is greater sensitivity to eye gaze adaptation in the structural encoding state ~170 ms but that the neural correlates of this effect are just not easily detectable in EEG measurements. Possibly, the neural sources that are affected by prior gaze direction information are located in a way parallel to the scalp surface which would make it difficult to (fully) measure their activity by EEG scalp electrodes.

Considering this possibility it might be worth replicating the present gaze adaptation experiments measuring magnetoencephalographic correlates of adaptation. The magnetoencephalographic M170 and the electroencephalographic N170 component have been discussed as originating from the same underlying neural sources (Deffke et al., 2007), the M170 has also been shown to be sensitive to eye gaze information (Watanabe, Kakigi, & Puce, 2001), and a recent study reported larger M170 amplitudes in response to averted as compared to direct gaze (Sato, Kochiyama, Uono, & Yoshikawa, 2008).

As the MEG method is only sensitive to the magnetic fields resulting from the electric currents in neurons oriented in parallel to the scalp surface, it is possible that gaze adaptation effects would be more pronounced in the M170 than in the N170. On the other hand, a similar lack of strong effects in an MEG study might allow the complete exclusion of the existence of large effects of gaze direction-specific adaptation in the time range of ~170 ms. Therefore, combined findings from EEG and MEG studies that provide a more detailed view on the activity of neural sources oriented both in a parallel and perpendicular way might be necessary to finally decide on the role of the structural encoding or ‘eye detecting’ in early gaze adaptation.

The time interval of 250 – 350 ms was consistently found to be affected by gaze adaptation in both Experiments 1 and 2. In Experiment 1, test faces of all three gaze directions elicited less negative amplitudes when presented following left as compared to right adaptation. This effect of adaptation direction was restricted to right-posterior electrodes. In Experiment 2, the analysis of the same time interval revealed significantly less negative amplitudes in response to direct gazing test stimuli than to test stimuli with left or right gaze in trials following adaptation to direct as compared to right gaze direction. Similarly, right gazing test stimuli following adaptation to right gaze direction evoked less negative amplitudes than test stimuli gazing to the left or directly at the observer. This pattern, however, was weaker than the one found for test stimuli with direct gaze following adaptation to that direction and failed to reach conventional levels of significance.

Although both Experiment 1 and Experiment 2 suggested an ERP effect of gaze adaptation in the 250 – 350 ms time interval, the precise pattern of gaze adaptation effects in the two experiments differed somewhat. In Experiment 1, adaptation to left gaze direction consistently evoked smaller negativities in response to test stimuli of all gaze directions over posterior, right-hemispheric electrodes. The restriction of this finding to right hemispheric electrodes is in line with studies reporting an advantage of the left visual field in gaze direction perception (Ricciardelli, Ro, & Driver, 2002) or greater right STS activity in response to direct as compared to averted gaze perception (Conty et al., 2007) stressing the role of the right hemisphere in the processing of face-related information.

When evaluating and interpreting the results of Experiment 1 it might be important to consider the later findings of Experiment 3 on the temporal persistence of eye gaze adaptation effects. Here, gaze adaptation effects were found to gradually decrease over time but to still be measurable several minutes after adaptation. Considering that the order of left and right gaze adaptation blocks was counterbalanced across participants in Experiment 1, it seems plausible to assume a residual influence of the first adaptation condition on the second one. Most probably, however, this affected the ERP data obtained following adaptation to left and right gaze to the same extent. The differences in the ERPs in response to left and right adaptation might therefore even be more pronounced than they appeared to be in the ERP data of Experiment 1.

The gaze adaptation effect observed in the same time interval in Experiment 2 was qualified by the gaze direction of the test stimulus. Here, amplitudes evoked by test stimuli gazing in the adapted direction were found to be less negative than amplitudes evoked by test stimuli gazing in unadapted directions. This was true for both direct and right adaptation conditions although the effect did not reach statistical significance in the latter case. This finding might be considered to reflect a reduced neural activity evoked by the presentation of a stimulus characteristic that has formerly been adapted to. Therefore, this effect might be interpreted to represent the relatively easier or ‘prepared’ processing of a gaze direction that had been extensively presented before test stimulus presentation. It is important to consider, however, that the behavioural results obtained in Experiment 2 suggested that adaptation to direct gaze does not produce any adaptation effects. It can therefore be speculated that the ERP results following direct gaze adaptation were not influenced by adaptation but rather represent the ‘normal’ response pattern obtained for test stimuli of left, direct, and right gaze direction. This pattern does not seem to differentiate between left, direct and right gaze, but rather seems to respond differently when presented with direct vs. averted gaze with significantly less negative amplitudes in response to direct as compared to averted gaze.

Consistent with this assumption, ERPs evoked by right gazing stimuli presented after adaptation to right gaze direction (which makes them more likely to be perceived as direct gazing) seemed to show a similar response pattern as test stimuli with direct gaze without prior adaptation (i.e. following direct gaze adaptation). Overall, this finding suggests that the distinction between direct and averted eye gaze might take place or at least influence processing in the time interval of 250 – 350 ms with direct gaze or gaze that is *perceived* as direct as a consequence of adaptation evoking less negative amplitudes than averted gaze.

In order to understand the different results of Experiments 1 and 2 as observed in the time interval of 250 – 350 ms, it might be important to recapitulate the major differences in the design of the two studies. For a start, there were different numbers of participants tested in Experiment 1 (N = 10) and Experiment 2 (N = 19) possibly suggesting the results of Experiment 2 to be somewhat more reliable than those of Experiment 1.

Second, there were different control conditions used in the two experiments. Whereas the effects of adaptation were compared to a pre-adaptation baseline phase in Experiment 1, they were compared to those of adaptation to direct gaze in Experiment 2. The change of the control condition allowed the judgement of the ERP correlates of gaze adaptation in Experiment 2 without the impact of stimulus repetition that strongly influenced the pattern of data recorded in Experiment 1. Therefore, the ERP data of Experiment 2 might be considered as more clearly representing the correlates of eye gaze adaptation.

Third, participants in Experiment 1 adapted to both left and right gaze direction, whereas Experiment 2 only investigated the effect of adaptation to right direction. The decision to have participants adapt to only one direction in Experiments 2 and 3 was based on the suspicion that gaze adaptation effects might survive a relatively long time interval, and was made to rule out possible effects of cancellation. The findings of Experiment 3, which revealed that gaze adaptation effects can survive a time interval in the range of several minutes, might suggest that the ERP data for adaptation to left and right gaze direction obtained in Experiment 1 might also have been affected by the preceding test block. The choice of having participants adapt to only right gaze direction in Experiment 2 was driven by the observation that adaptation effects on right gazing stimuli were numerically (though not statistically) weaker in both the study by Jenkins et al. (2006) and in Experiment 1 reported here, and was therefore considered to be the most conservative one. However, this difference in the experimental designs of Experiments 1 and 2 makes it particularly difficult to compare their results especially with regard to the effects of adaptation to left gaze which had a prominent role in the time window of 250 - 350 ms in Experiment 1 but had not been tested in Experiment 2. Considering the temporal persistence of gaze adaptation effects, further studies using longer breaks between adaptation sessions of different gaze directions and implementing direct gaze adaptation as a control condition will be required to obtain a deeper understanding of the differences between adaptation to left and right gaze direction.

Fourth, Experiment 1 used faces with large gaze deviations (25°) as adaptation stimuli, whereas adaptation stimuli in Experiment 2 depicted faces with relatively small (10°) gaze deviation. Similarly, test stimuli used in Experiment 1 consisted of faces with only very small, i.e. 5° gaze deviations while test stimuli in Experiment 2 showed faces with small (5°) and larger (10°, i.e. corresponding to the adaptation stimuli) gaze deviations. The use of perceptually similar adaptation and test stimuli in Experiment 2 aimed at a reduction of possible recovery of adaptation. Moreover, the finding that reliable adaptation effects could be elicited by adaptor faces with eye gaze deviating by only 10° from direct gaze even if test faces showed the very same deviance in gaze direction allowed new and deeper insight into the nature of adaptation effects. However, considering a possible comparison of the ERP results obtained in Experiments 1 and 2, the different adaptation stimuli used raise the problem that the behavioural adaptation effects obtained in the two experiments were of a very different magnitude. The behavioural results of Experiments 1 and 2 as well as the data by Calder et al. (2008) strongly suggest that adaptors with large gaze deviances produce larger aftereffects than do adaptation stimuli with only small gaze deviations. This makes the adaptation effects observed in Experiments 1 and 2 at least quantitatively different, which might lead to difficulties when trying to compare their neural correlates. Considering the possibility that eye gaze direction may be coded in a multichannel-system as proposed by Calder et al. (2008) it is also possible that adaptation effects elicited by 25° and 10° adaptation stimuli are even qualitatively dissimilar, as they might be produced by different neural populations selectively coding relatively small and relatively large gaze deviations.

Overall, whereas the specific reasons for the discrepancy in adaptation effects between Experiments 1 and 2 must remain unclear at present, both studies clearly suggest processing mechanisms involved in the perception of faces ~250 – 350 ms post stimulus onset to be sensitive to gaze adaptation. From fMRI studies in humans (Haxby et al., 2000; Hoffman & Haxby, 2000) as well as from single cell recordings in monkeys (Perrett et al., 1985), it is known that the STS region plays a prominent role in gaze perception. When assuming that the activity recorded in the time interval between 250 – 350 ms at least partly reflects activity in STS structures, Experiment 1 suggests the *right* STS to be sensitive to the preceding directional gaze context (left vs. right direction) irrespective of the actual gaze direction of the test stimulus. The results of Experiment 2, however, suggest that cells in the *bilateral* STS show a more systematic response pattern. Here, test faces were observed to elicit larger positivity when their gaze is directed in the same direction as had previously been observed in the adaptation stimuli. To my knowledge, no ERP study investigating the perception of eye gaze has so far reported effects of different gaze directions or more general effects of direct vs. averted gaze in this time window, and it is therefore difficult to relate the present findings to those of other investigators.

In Experiment 2, large effects of gaze adaptation have also been observed in a late positive component over frontal, central, and parietal electrodes. Here, amplitudes in response to test stimuli with eye gaze averted in the adapted direction evoked significantly smaller, i.e. less positive amplitudes than test stimuli gazing in the unadapted directions. This finding might possibly reflect a P3 effect. These effects have traditionally been reported in oddball paradigms in which different stimuli are presented in a random sequence with one of them, the standard stimulus, being presented more frequently than the second one, the deviant or target stimulus. Typically, the rare deviant stimulus elicits a positive going component with a central scalp distribution over the midline electrodes Fz, Cz, and Pz, which has been described as increasing from frontal to parietal electrode locations (Johnson, 1993).

Sutton et al. (1965) suggested ‘information delivery’ to be the critical feature eliciting the P3. They proposed that participants gain ‘more information’ from a rare, deviant stimulus than from the standard stimulus which is more frequently presented and may therefore be expected. Findings concerning the effects of stimulus probability seem to underline the relevance of the ‘information delivery’ theory as increasing target stimulus probabilities have been shown to produce decreasing P3 amplitudes (e.g. Polich & Bondurant, 1997). Another theoretical account on the P3 is the context-updating theory (Donchin, 1981) which assumes that the P3 reflects the activity of an attentional process that leads to an update of a stimulus representation in working memory whenever a new stimulus is detected which does not match the context given by the preceding stimuli.

Obviously, the standard oddball paradigm differs widely from the experimental paradigm used in Experiment 2. Although participants did not have to respond to all faces presented, ‘targets’ requiring a response appeared regularly and were announced by a question mark and not defined by a certain feature that would require a response and was absent in ‘non-targets’. Further, many different facial identities displaying different gaze directions were used as stimuli, therefore leading to a more complex paradigm than using only two different stimuli. However, given that test phases were preceded by adaptation blocks and each test face was preceded by additional top-up adaptation stimuli it appears plausible to claim that there was a ‘standard’ context provided by the respective adaptation condition and represented in more than 2/3 of the faces presented. Due to this standard context, test stimuli displaying gaze directed in unadapted directions might be considered as ‘deviant’ stimuli. The pattern observed in the late positive component might therefore reflect the smaller information delivery or relatively easier context update of test stimuli with gaze directed in the adapted direction. When considering the late adaptation effect as a correlate of ‘context updating’ or ‘information delivery’, one might suggest that the response pattern at this late stage represents the neural indicator of 'novelty detection' which has been described as one of the consequences of perceptual adaptation.

One possible prediction derived from this application of the context update or information delivery explanations of the P3 on the adaptation effects observed in the late positive component could be the following: test stimuli identical to the adaptors, i.e. showing the same 10° deviance from direct gaze, might be expected to be more easily integrated or to deliver less information than stimuli with eye gaze deviating only 5° in the adapted direction. However, the statistical analysis of the ERP results in the late time window did not reveal an interaction with the deviance of a test stimulus. This insensitivity to different gaze deviances in the same direction might arise from the fact that the effect was found at a relatively late, post-perceptual processing stage where the gaze perception stimuli might be categorised or semantically coded in terms of 'gazing left' or 'gazing right' rather than in terms of the exact physical pattern of the stimulus. It has to be kept in mind, however, that this interpretation of the late gaze adaptation effect is a post hoc interpretation that certainly requires further research in order to reject or strengthen the hypotheses described above.

7.3 Temporal aspects of eye gaze adaptation

Aiming at a deeper understanding of the nature of eye gaze adaptation, Experiment 3 investigated the time-course of gaze adaptation effects. A series of two experiments revealed a higher initial level and a more gradual decay of aftereffects for 5° than 10° test stimuli. In both cases the nature of the decay could be well modelled by exponential decay functions which have earlier been described for adaptation to basic physical stimulus attributes (Hershenson, 1989; Petersik, 2002). This analogy further stresses the similarity of the neural mechanisms underlying the established adaptation effects to basic stimulus attributes and the relatively recently discovered high-level adaptation effects.

What is difficult to conclude, however, from Experiment 3 is the question of which further factors apart from the deviance of the gaze direction possibly influence the decay rate of gaze adaptation effects. More precisely, an interesting question for future research might be whether the number of intervening face stimuli presented after the last display of an adaptation stimulus determines the persistence of gaze adaptation effects. A well-known characteristic of perceptual aftereffects in low-level vision is the so-called *storage* of an effect which was first described for movement aftereffects (Wohlgemuth, 1911; cited from Verstraten, Fredericksen, Grüsser, & van den Grind, 1994). This term describes the effect that the temporal decay of adaptation is delayed or interrupted when test stimuli are not presented immediately after the adaptation phase, e.g. when participants are instructed to close their eyes after adaptation. Moreover, storage effects have even been shown to occur when another visual pattern is presented between adaptation and test phase (Verstraten et al., 1994). Considering these findings, it seems promising to investigate whether the decay of gaze adaptation effects is time-locked, i.e. whether it decreases over time independent of the visual input provided after adaptation. However, bearing in mind the results of earlier studies on movement adaptation described above, it seems more plausible to assume that the decay of aftereffects is to a large degree stimulus-locked, i.e. a certain number of intervening stimuli might be necessary for the effect to decay.

The finding that gaze aftereffects may survive a time interval of several minutes is somewhat surprising, especially when taking the level of changeability of eye gaze information into account. However, considering the slight asymmetries contained in human faces and especially in their eye position (Güntürkün, 1991), it seems sensible to recalibrate the perception especially of smaller gaze deviations according to earlier experiences with gaze direction. Eye gaze that is farther averted is usually much easier to integrate and the information derived from both eyes is more consistent. Therefore, less stable adaptation effects might be sufficient in order to recalibrate this kind of gaze direction. If the differential time-courses of adaptation observed in Experiment 3 really reflect the greater need for a ‘fine tuning’ of the perception of smaller as compared to larger gaze deviations, a clear prediction for a future study might be that gaze direction adaptation effects should be more stable in intra-identity trials, with adaptor and test faces always displaying the same person, as compared to inter-identity trials with adaptor and test faces displaying different identities and therefore not allowing for a ‘fine tuning’ of gaze detectors to the individual morphometry of one single person.

An important aspect that is related to the above-named hypothesis of a more stable recalibration of relatively small 5° gaze deviations as compared to larger 10° gaze deviations is also of general relevance for all of the behavioural results on eye gaze adaptation that have been reported in the present thesis. In line with the earlier studies on gaze adaptation (Jenkins et al., 2006; Seyama & Nagayama, 2006) the paradigms used in Experiments 1, 2, and 3 required participants to categorise the gaze direction of a presented test face by pressing one of several response keys representing a certain gaze direction. Response options were the classification of the gaze direction as “left”, “direct”, or “right”. It has to be considered that the magnitude of aftereffects especially in response to test stimuli with larger gaze deviation might have been underestimated by choosing this response set. Theoretically speaking, if adaptation to right gaze direction generally reduced participants’ ability to perceive that direction by 5°, they would classify test stimuli actually gazing 5° to the right as showing direct gaze, whereas they would perceive test stimuli actually gazing 10° to the right as gazing only 5° to that direction and therefore still classify them as gazing right. That is, although the magnitude of the aftereffect in terms of the shift in perception would be exactly the same, the above-named example would lead to behavioural data suggesting a gaze adaptation aftereffect to arise in response to the 5° test stimuli and no aftereffect at all in response to the 10° test stimuli.

The above-named theoretical problem might be solved by finding a way to measure induced shifts in the perception of gaze direction in a continuous manner giving the participants more than just “left”, “direct”, and “right” response categories. For practical reasons, however, it seems difficult to use a purely continuous measurement as such a procedure would necessarily have to be more complicated and time consuming than the response options used in current studies. Given that aftereffects are known to decrease as a function of the inspection time of the test stimulus (Leopold et al., 2005), a fast response option that does not require participants to look away from the screen will be necessary in order to capture the aftereffect on its early and maximal stage. A compromise in terms of practicability and accuracy might be to give participants five or more response options instead of three.

A further aspect related to the effects observed in Experiment 3 is the question as to what extent adaptation effects to different face-related characteristics (i.e. identity, eye gaze direction, emotional expression, gender) are characterised by different decay rates. The most influential models of face perception (Bruce & Young, 1986; Haxby et al., 2000) both stress that some aspects of faces are largely changeable and allow for an analysis of the momentary cognitive, attentional, and emotional state of a person (e.g. eye gaze direction, emotional expression) whereas other aspects are relatively stable over time (e.g. the structural composition or gender of faces) and allow for the recognition of familiar faces irrespective of their viewpoint or current expression. Haxby et al (2000) proposed that these characteristics of face perception are processed by a distributed neural system in which invariant and changeable aspects are being analysed by different structures. It is therefore plausible to assume that adaptation to different aspects in faces is characterised by different decay rates, with adaptation to more stable aspects being relatively long-lived and adaptation to changeable aspects being subject to faster decay.

Preliminary evidence for this assumption can be derived from a comparison of the data obtained in Experiment 3 to a recent study on effects of identity adaptation on familiar faces using a variation of the FDAE (Carbon et al., 2007). In this study, participants adapted to configurally manipulated famous faces and the effects of adaptation were examined after five minutes or 24 hours after adaptation, respectively. Carbon et al. (2007) found effects of adaptation to manipulated famous faces both five minutes and - weaker but still significant - 24 hours post adaptation. This provides first evidence for very long-lasting effects of adaptation to spatial manipulations, and suggests that adaptation to relatively stable face characteristics (i.e. their structural configurations) is long-lasting relative to the aftereffects lasting for minutes which could be observed for the changeable feature of gaze direction in faces in Experiment 3. As Carbon et al. (2007) consistently used only one test phase, either five minutes or 24 hours after adaptation, a precise tracking of the decay of the aftereffect and its modelling could not be performed. It might be worth conducting further studies containing several post-adaptation phases in order to allow for an observation of the aftereffects from their initial maximum until they have completely vanished.

7.4 Effects of adaptation to face and voice gender

Experiment 4 was conducted to test the applicability of the newly developed control condition of ‘neutral adaptation’ in an adaptation paradigm investigating the perception of another facial feature apart from eye gaze direction. The study investigated the neural correlates and the degree of modality invariance of gender adaptation effects examining the effects of adaptation to both face and voice gender and provided the first evidence for cross-modal adaptation effects. Both adaptation to male faces and male voices led to an increased probability to perceive subsequently presented gender-ambiguous test faces as female. This study therefore suggests that gender adaptation effects at least partly reflect the recalibration of a superordinate, modality invariant level of gender representations. It is important to note, however, that whereas an earlier study on voice gender adaptation found clear evidence for adaptive recalibration of the perception of gender in voices in intra-modality trials (i.e. when adaptor and test stimuli both consisted of human voices) cross-modal effects of adaptation to gender in faces on the perception of gender-ambiguous voice stimuli were absent in this study (Schweinberger et al., 2008).

Further, it has to be considered that the statistical analyses suggested the cross-modal (i.e. voice-to-face) adaptation effects in Experiment 4 to be somewhat weaker and possibly less reliable than the unimodal face adaptation effects. Bearing in mind the conflicting result of the earlier voice gender adaptation study (Schweinberger et al., 2008) and the somewhat unclear statistical results on voice to face gender adaptation in Experiment 4, it is obvious that these findings require replication.

Supposing that the findings of cross-modal adaptation can be replicated in future studies, gender information contained in human voice samples appears to have an influence on how participants categorise subsequently presented face stimuli according to their gender. This finding suggests that adaptation does not only influence a modality-specific representation of the gender of a person, but that some sort of adaptive recalibration of gender perception also takes place at a higher, modality-invariant level of person representation. This finding is of special interest as Kovács et al. (2006) recently reported that adaptation to gender in hands, although leading to aftereffects on the perception of gender in subsequently presented hand stimuli, did not evoke aftereffects in the perception of gender in faces.

The different findings in the voice-to-face adaptation and hand-to-face adaptation studies might be partly due to differences in the relevance of voice and hand information for gender discrimination. Participants might generally be more experienced in judging the gender of a person from his or her voice rather than the person's hand. In everyday life much interpersonal communication takes place on the telephone where the only available physical information concerning the interlocutor is his or her voice and people are usually very confident in judging the person's gender when talking to an unknown person. It is therefore possible that people are very experienced and efficient in extracting person-related information from voices. Further, it is most likely (and is even considered a principle of common politeness) that people who are talking to each other in a face-to-face situation look at each other so that face and voice information are often perceived at the same time. Studies on audio-visual integration have described the relevance of the co-occurrence of face and voice information. For instance, the observation of face information (i.e. facial movements) has been shown to enhance speech perception, especially under noisy conditions (Rosenblum, Johnson, & Saldana, 1996; Schwartz, Berthommier, & Savariaux, 2004). Moreover, under certain circumstances visual speech has even been shown to alter the perception of auditory signals: conflicting visual and auditory information has been found to make us *hear* a syllable that has never been said but is merely a blend of the auditory and visual signals presented – a phenomenon known as the McGurk effect (McGurk & MacDonald, 1976).

Whereas these findings stress that voice information has to be considered as an important aspect of everyday encounters, both presented in isolation, as for example in communications over the phone, and in simultaneous occurrence with face information, visual hand information does not play a similarly important role in human everyday life. Although hand gestures are an important aspect of non-verbal communication and have even been shown to be able to improve our speech comprehension (e.g. Holle & Gunter, 2007), we do not perceive faces and hands simultaneously with the same frequency as faces and voices. Moreover, different from voice information, we are rarely confronted with hands in isolation, i.e. in the absence of faces. These circumstances might explain the findings that adaptation to voice gender information seems to have an effect on the perception of face gender, whereas adaptation to hand gender information does not (Kovács et al., 2006).

An interesting test on this theory might be a replication of the cross-modality adaptation study by Kovács et al. (2006) comparing the results obtained with normal hearing participants to those collected in a population of deaf and dumb persons. People who were born deaf usually communicate via a sign language. Therefore, their communication mainly relies on attention to and interpretation of hand gestures which are usually performed in front of the interlocutor’s face providing simultaneous presentation of hand and face information. This might lead to the effect that this group usually pays more attention to other people’s hands and should therefore be more sensitive to information derivable from them.

Another interesting question related to the finding of voice to face adaptation effects arises from their comparison to the results reported by Schweinberger et al. (2008). Here, adaptation to the gender of silently articulating faces presented in videos did not have an effect on the gender classification of subsequently presented voices. Assuming that cross-modal adaptation takes place at a very high level of person categorisation as suggested by the findings in Experiment 4, it seems unlikely that the general use of videos instead of static photographs of faces explains the conflicting findings. However, as the videos presented silently articulating faces (i.e. no sound was presented along with the videos) it may be possible that participants' attention was especially attracted by the moving mouth region of the faces and that they therefore processed the faces differently from static images or articulating faces presented with sound.

As mentioned in greater detail in the introduction part of this thesis, a number of factors have been found to be important for the perception of gender in faces: next to colour (Hill et al., 1995) and luminance information (Frost, 1988; Russell, 2003) some featural aspects have been found to differ systematically between the two sexes: the eye region and the facial outline (Brown & Perrett, 1993; O'Toole et al., 1998; Yamaguchi et al., 1995), the size of the nose, and the prominence of the eyebrows (Campbell et al., 1999; Enlow, 1982). The importance of the eye region for gender discrimination was further emphasised in studies concerning the structural differences between male and female faces, showing that the distance between the brow and the upper eyelid is one of the most reliable structural cues to gender in static faces (Brown & Perrett, 1993; Campbell et al., 1996; Campbell et al., 1999).

Considering these findings, it seems possible that the presentation of silently articulating adaptor stimuli might have attracted participants' attention to the moving mouth regions of the adaptor faces, where they possibly tried to lip-read the expression of the stimuli as there was no acoustic information present. In a study examining the influence of task on gaze patterns during silent speech-reading, Lansing and MacConkie (1999) found that whereas participants who were instructed to discriminate whether a silently articulating person made a statement or asked a question directed 39.5% of their gaze fixations to the upper facial (eye) region, they only directed 14.4% of their gaze fixations to that region when their task was to identify the spoken words. Similarly, participants in the study of Schweinberger et al. (2008) might not have processed the eye and brow regions which have been shown to be of high relevance for the identification of face gender as deeply as in static stimuli. Although it can certainly be assumed that participants were still able to extract the gender of the adaptation stimuli given their relatively long presentation duration (~900 ms) the distraction of participants' attention from the eye region and an overrepresentation of attention allocation to the mouth region of the adaptation stimuli might have prevented participants from activating strong gender representations and might therefore have inhibited cross-modal gender adaptation.

Another possibly important difference between Experiment 4 and the cross-modal adaptation study conducted by Schweinberger et al. (2008) is the different ecological validity contained in the procedure. In Experiment 4, participants adapted to voice adaptation stimuli before being presented with static and obviously silent (closed mouths) test faces. This resembles situations we encounter daily as we often hear voices without seeing their faces or look at people who do not speak at that time. Even when talking to people there are usually breaks in the conversation with moments of silence before a new topic is addressed. The participants judging the gender of test voices in the study by Schweinberger et al. (2008), however, were presented with a different scenario: Following the somewhat artificial situation of perceiving silently articulating faces, they were presented with the test voices after a time delay of 500 ms. In everyday life, however, we never see a person pronounce a syllable which we only hear with a delay of 500 ms. A possible test of this post hoc theory might consist of a study comparing the current cross-modal adaptation condition using silently articulating videos to a new cross-modal adaptation condition which might be of higher ecological relevance: if the suggested explanation should be at least partly responsible for the fact that Schweinberger et al. (2008) did not find a cross-modal adaptation effect, then adaptation to static images of faces might be expected to have an effect on the perception of gender in voices.

A number of studies on audiovisual speech integration has investigated the question of how asynchronous auditory and visual signals are perceived and tried to identify a threshold for the detection of desynchrony. In the case of the auditory signal being delayed with respect to the visual stimulus, a time range of about 250 ms has been identified to severely disrupt the perception of synchrony (Dixon & Spitz, 1980; Munhall, Gribble, Sacco, & Ward, 1996). It is possible that the timing of the visual adaptation and auditory test stimuli is also of relevance with regard to the paradigm used by Schweinberger et al. (2008). The 500 ms interval between the last visual adaptation stimulus and the auditory test stimulus as used here might have stressed the fact that face and voice stimuli were unrelated and might therefore not have led to cross-modal gender adaptation. Although adaptation and test stimuli would necessarily have to be presented separately, some cross-modal adaptation may have had occurred at an ISI shorter than 500 ms.

Consistent with the combined findings of Experiments 1 and 2, the analysis of the ERP data obtained in Experiment 4 and their comparison to earlier ERP studies on gender perception (Kovács et al., 2005; Kovács et al., 2006; Kovács et al., 2007) revealed an overlap of contributions of general face adaptation processes and correlates of the specific adaptation to face gender in the N170 component. The implementation of a control condition using androgynous adaptation and top-up stimuli led to a substantial decrease of the N170 amplitude differences observed in earlier studies. The modality effect observed in this component was of similar magnitude as the N170 effects observed by Kovács et al. (2006), suggesting that the latter might have been strongly driven by effects of repeated face presentations vs. face stimuli preceded by non-face control stimuli or black screens, respectively.

However, this interpretation can only be speculative as Experiment 4 only compared the presentation of faces following black screen presentation (which was the visual ‘stimulus’ accompanying the presentation of the auditory adaptor) to the presentation of faces following androgynous or male face adaptor presentation. The use of a third condition with visual (non-face) control stimuli similar to those that Kovács et al. (2006) presented before the test face would have been sensible in order to allow for a more direct comparison of the results of Experiment 4 to those of Kovács et al. (2006). However, the experimental design of Experiment 4 allowed for an estimation of gender adaptation effects in the N170 component without a differential effect of face repetitions. These gender effects were relatively small and restricted to one homologous pair of electrodes with test stimuli evoking smaller N170 amplitudes after male than after androgynous adaptation at electrode PO9 and evoking larger amplitudes after male than androgynous adaptation at PO10.

The fact that adaptation to androgynous vs. male faces evoked differential effects in the left and right hemisphere can be partly reconciled to a recent study investigating the relative contributions of the left and right hemispheres to gender discrimination. Parente and Tommasi (2008) tachistoscopically presented chimeric faces created by juxtaposing left and right half-faces of different genders. Participants were asked to classify these stimuli according to their gender. The authors calculated an index of laterality to determine whether participants decided more upon the left or the right part of the stimulus and found a right-hemispheric advantage for gender recognition but only for female faces: judgements were significantly more based on the left hemi-face but only for those stimuli that consisted of a left female and a right male half-face. Taken together, the findings of Parente and Tommasi (2008) and those obtained in Experiment 4 of the present thesis might be considered to hint at a special role of the right hemisphere in female face processing.

Considering that test faces were more likely to be judged as female following adaptation to male faces, the larger N170 amplitudes which were measured over right-hemispheric electrodes in response to test faces following male as compared to androgynous adaptation might also be considered as representing deeper processing of femaleness. Due to the fact that participants in Experiment 4 only adapted to faces of one gender (apart from the neutral control condition) it is impossible to further challenge the idea of laterality in gender perception by comparing the ERP correlates of male and female gender adaptation. Moreover, it has to be noted that the majority of participants in Experiment 4 was of female gender (16 out of 19). As it is known that participants are usually more efficient in processing faces of their own gender (own gender bias, see e.g. Wright & Sladden, 2003) the prominent role of the right hemisphere in female gender processing might be restricted to female participants. Future studies investigating equal numbers of male and female participants and testing the effects of adaptation to both male and female gender might reveal deeper insight into what can only be a vague post hoc explanation on the basis of the present results.

Largest effects of gender adaptation were observed in the late positive component over central and parietal electrodes. Here, test stimuli preceded by male face adaptors elicited significantly more positive amplitudes than those preceded by androgynous adaptors. This effect was restricted to unimodal adaptation trials and could not be observed in response to test faces following voice adaptors.

The late positive effect closely resembled the one obtained in Experiment 2 in which test stimuli gazing in the adapted direction were found to elicit smaller, i.e. less positive, amplitudes than test stimuli gazing in unadapted directions. This pattern was interpreted as representing a P3 effect reflecting the relatively easier context update or smaller information delivery of test stimuli that most closely resembled the context given by the adaptation stimuli as compared to test stimuli that deviated from the given context. The results observed in Experiment 4 might similarly have been predicted by the rationale assumed to underlie the effect in Experiment 2. Given that

50% of the test stimuli were very close to androgynous (40%/60% and 60%/40% male/ female proportion) and 25% of the test stimuli were relatively masculine (80%/20%) and relatively feminine (20%/80%), respectively, the overall deviance of test stimuli from adaptation stimuli was smaller in the androgynous face adaptation condition than in the male adaptation condition. This might have led to a relatively easier context update or smaller information delivery of test stimuli following androgynous than male adaptation, reflected in smaller, i.e. less positive amplitudes to test faces following androgynous than male adaptation.

To test this interpretation, separate analyses were conducted to investigate the magnitude of the late positive effect for the different morph levels of test stimuli. Following the hypothesis of easier context update or smaller information delivery of those test stimuli that are most similar to the context provided by the adaptation and top-up stimuli, it was predicted that the P3 effect should be largest for the largest perceptual difference, i.e. for relatively female test stimuli following male as compared to androgynous adaptation and smallest for relatively androgynous test stimuli following androgynous adaptation. The analyses revealed a significant effect, however, only for the relatively feminine stimuli, i.e. test stimuli of the morphlevel 20% male/80% female, which produced significantly larger positivity following male than androgynous face adaptation. For all other morphlevels amplitudes evoked between 400 and 600 ms did not significantly differ between androgynous and male adapted trials.

It is difficult to finally decide on the nature of the late effects observed in Experiments 2 and 4, especially as the examination of the post-hoc explanation in a detailed analysis for the different morphlevels of test stimuli in Experiment 4 did not exactly reveal the predicted pattern. However, it has to be noted that the only significant effect found in this analysis was found for the relatively feminine test stimuli following male as compared to androgynous adaptation and therefore for the test stimulus class that was most dissimilar to the male face adaptors. Given that the late effect observed in the eye gaze adaptation paradigm applied in Experiment 2 did not differ for stimuli deviating 5° vs. 10° from direct gaze, the findings of both experiments might be reconciled to the idea that the late effect does not differentiate between smaller perceptual differences in the stimuli but might rather operate on a more global, semantically driven concept of ‘left’ and ‘right’ or ‘male’ and ‘female’ categories, respectively.

7.5 Summary and outlook

To sum up, the present series of experiments replicated and extended earlier findings on high-level face adaptation effects. Experiment 1 revealed a first insight into the neural correlates of gaze adaptation effects and suggested that direction-specific effects emerge not earlier than ~250 – 350 ms post stimulus onset. Further, the findings of that study proposed that the neural processing stages eliciting the N170 component are largely sensitive to face repetition as reflected in dramatically reduced N170 amplitudes in trials immediately following prior face presentation as compared to trials presented after longer intervals of a blank screen.

These observations motivated the application of a new control adaptation condition in Experiment 2 in which participants either adapted to direct gaze or to right gaze direction, therefore being presented with the same amount of face information in both conditions. The newly implemented direct gaze adaptation condition was found to lead to the same judgements of the direction of gaze in test faces as observed in a traditional pre-adaptation baseline. This suggests that the direct gaze adaptation condition served the purpose of a neutral control condition. N170 results in Experiment 2 were unaffected by general face adaptation effects in line with the hypothesis that the large N170 effects observed in Experiment 1 had been due to general face adaptation. The finding that only very small effects of gaze adaptation could be found in the N170 in Experiment 2 whereas correlates of gaze adaptation were more pronounced in the time interval of 250 – 350 ms can therefore be considered as further evidence that adaptation to gaze does not alter the processing of face stimuli before 250 ms. Largest effects of gaze adaptation were observed in the late positive component ~400 to 600 ms after stimulus onset, where test stimuli gazing in the direction of adaptation were found to elicit smaller amplitudes than test stimuli gazing in unadapted directions. This pattern was interpreted as reflecting a P3-like effect in terms of an easier context update or smaller information delivery of adapted stimuli, leading to an emphasis of relatively new, i.e. unadapted, characteristics in faces which has been believed to reflect the neural basis of ‘novelty detection’ as a consequence of adaptation.

Experiment 3 investigated the time-course of gaze adaptation. Adaptation effects observed in response to test stimuli with small gaze deviations were characterised by a higher initial level and a more gradual decay than stimuli with larger gaze deviations. The decay of aftereffects in the perception of both small and larger gaze deviations was found to be best described by a negative exponential function further stressing the similarities in the characteristics of low-level and high-level adaptation processes.

Finally, Experiment 4 investigated the effects of adaptation to gender in voices and faces on the perception of facial gender. The study provided the first evidence for a cross-modal adaptation effect as adaptation to male voices was found to bias the classification of gender of subsequently presented face stimuli. Only small correlates of gender adaptation could be observed in the N170 component whereas a more systematic pattern was found in the time range of the late positive component ~400 – 600 ms after stimulus onset. Here, test stimuli evoked more positive amplitudes when presented following male as compared to androgynous adaptation. Separate analyses for test faces with different male/female proportions revealed that this effect was most pronounced for relatively female test stimuli. This finding supported the idea that the late effect might reflect the ease of integration of test stimuli in the context provided by adaptation stimuli. In line with the findings of Experiment 2, this effect seemed to be based on a categorical decision on “maleness” and “femaleness” and did not differentiate between the smaller variations of gender in test stimuli.

The findings of very small yet statistically significant effects in the N170 in Experiments 2 and 4 suggest that small differences were reliably evoked in most of the participants. The comparison of N170 effects found in Experiments 2 and 4 to those observed in Experiment 1 and by Kovács et al. (2006), respectively, suggests that this component responds more strongly to adaptation to general face configurations than to gaze direction information or gender information. This finding can be reconciled with the current work of Itier et al. (2006), who tried to disentangle the relative contributions of general face and eye gaze information on the N170 component. They proposed that distinct populations of eye and face detectors contribute to the N170 component. In upright face perception they assume the facial parts to be configurally processed (i.e. in relation to each other) with only face-selective neurons responding, whereas eye-selective neurons are believed to be inhibited by face cells. When inverting a face, however, the inhibitory influence of face cells on eye cells is believed to be impaired which allows eye cells to respond to the eye region of the stimulus leading to the N170 amplitude increase usually observed in response to face inversion.

Whereas the data of Experiment 2 suggest *some* influence of the eye region on the N170 amplitude, the large reduction of the N170 effect observed between Experiments 1 and 2 certainly supports the hypothesis of Itier et al. (2006) claiming that the N170 in response to upright faces is mainly driven by general face information. An interesting prediction from the model proposed by Itier et al. (2006) would be that effects of gaze adaptation on the N170 should be more pronounced in a gaze adaptation paradigm using isolated eyes as stimuli. Similarly, adaptation to gaze direction in inverted faces might be expected to lead to selective adaptation of eye cells which would then be able to respond to the stimulus unaffected by the inhibitory influence of the face cells. Consequently, greater N170 effects of adaptation to eye gaze should be expected in this condition.

An important field for future research will be the investigation of the precise relationship between adaptation and priming. Although both processes are based on stimulus repetition, they lead to completely different response patterns. Whereas priming leads to faster and/or more accurate responses to stimuli that have been presented earlier, effects of adaptation usually reveal themselves in the form of inaccurate perceptions of test stimuli whose perception is usually biased away from the characteristics of previously presented adaptation stimuli.

One of the major differences between high-level face adaptation and face-related priming is the level at which the effects are assumed to occur. Whereas high-level adaptation is believed to be a perceptual effect affecting the sensitivity of cell populations selectively coding different aspects in faces (e.g. left vs. right gaze direction in the perception of eye gaze) priming is thought to occur at higher levels which are only accessed after the completion of structural face encoding. The Interactive Activation (IAC) model proposed by Burton, Bruce, and Johnston (1990) is based on the Bruce and Young model (1986) and assumes semantic priming to be a result of spreading activation between person identity nodes and person-related semantic information. Further, Burton, Bruce, and Johnston (1990) suggested that identity (i.e. repetition) priming results from a strengthening of the connection between face recognition units and person identity nodes. Therefore, Burton et al. (1990) believed person-related priming to occur at stages following the analysis of visual facial characteristics which they assume to be necessary for FRUs to be activated. This is consistent with the finding that face repetition priming does not seem to affect the N170 component but that priming effects are usually only detected from ~250 ms on

(Schweinberger et al., 2002). On the contrary, the N170 has consistently been shown to be largely affected by face adaptation (Kovács et al., 2006; Experiments 1, 2, and 4 of the present thesis) suggesting that face adaptation does at least partly take place at the structural encoding stage of face perception.

It is therefore possible to evoke effects of face adaptation and semantic priming in faces in the same experiment. For instance, when participants adapt to the picture of George Clooney (adaptation stimulus) and are subsequently presented with a face identity morph containing equal amounts of identity information of George Clooney and Brad Pitt (prime) they should be expected to respond faster to the subsequently presented image of Angelina Jolie (target) as compared to a condition when the prime consists of a morph containing equal amounts of identity information of Brad Pitt and Matt Damon. Due to identity adaptation, the prime stimulus in the former example would be perceived as Brad Pitt. This percept would trigger the ‘Brad Pitt FRUs’ therefore leading to access to the ‘Brad Pitt PIN’. According to Burton et al. (1990) the PIN activation would lead to activation of the semantic information about the actor, part of which should also be knowledge that he is related to Angelina Jolie. As the connections between semantic information and PINs are believed to be bidirectional, the PIN of Angelina Jolie would also be activated, leading to a faster response if her picture is subsequently presented as a target. In other words, adaptation mechanisms lead to a certain *percept*, the later processing of which might lead to priming.

A further difference between priming and adaptation studies consists in the timing of experimental parameters. Even within the area of adaptation studies it has been shown that short-term (500 ms) vs. long-term presentation (5 s) of adaptation stimuli seem to specifically modify different neural processes (Kovács et al., 2007) suggesting that timing is a crucial aspect. Whereas priming studies only briefly present prime stimuli, adaptation studies are usually characterised by long presentation durations of the adaptation stimuli (i.e. in the range of several seconds), maybe even by a long series of several successively presented adaptation stimuli. Adaptation effects for eye gaze direction have been shown to gradually decrease over time and to completely decay in the range of several minutes. Even when assuming that aftereffects for unchangeable aspects in faces are subject to slower decay, identity priming effects might generally be more robust with regard to long prime-target intervals and also with regard to the number of intervening visual stimuli (Bruce & Valentine, 1985) again suggesting that they might occur at a different processing level. Therefore, a systematic variation of the presentation duration of the first stimulus (prime/adaptor), of the time interval between the first and second (target/test face) stimulus, and the number of intervening stimuli might be a promising account in order to improve our understanding of the relationship of perceptual adaptation and priming.

A final aspect which should be addressed here is the functionality of adaptation effects. The fact that aftereffects of adaptation can be observed in the form of 'biases' in the perception of adapted features leads to a relatively negative or 'pessimistic' terminology suggesting that the phenomenon is merely a design fault of the visual system. However, in their review on the motion aftereffect Anstis, Verstraten, and Mather (1998) stress that

> *the naive view that neurons can 'fatigue' rather like over-exercised muscles, perhaps owing to depletion of neurotransmitters is almost certainly incorrect, since some neurons seem to resist adaptation altogether.* (p. 115)

The aspect that some neurons do show adaptation after prolonged exposition to a stimulus feature whereas others do not suggests that adaptation is a useful property of some neurons rather than some kind of mistake and indeed visual adaptation seems to be a very efficient tool in 'fitting our mind to the world'.

It is likely that the adaptive response pattern of neurons makes sure that our visual system is regularly 'reset', enabling us to have a stable perception of the world around us. The perception of many visual characteristics seems to be organised in relation to a norm, or null-point, which does not appear to be an absolute value but is rather frequently updated on the basis of the average activity on that characteristic. This regular updating mechanism makes our visual system very flexible and allows an efficient adjustment of neural coding mechanisms to the stimulus characteristics that actually surround us.

Phenomena in face perception, such as the *own-race bias* seem to be a result of adaptation. Although generally able to process, learn and recognise each of the ~6.5 billion faces which are factually present on this planet, our face recognition system usually 'concentrates' on those faces that are available and of relevance to our daily lives, which makes us experts in their identification. However, as has been shown in studies investigating the own-race bias in people who left their homelands to live in other countries with a different ethnic composition, our visual system is very flexible and able to adapt to the new visual context; the own-race bias slowly decreases over time (Chiroro & Valentine, 1995). This is especially astonishing when considering that long distances were very difficult to overcome even only 100 years ago. Times have changed and countries with a very different ethnical composition can be reached in as short as a 12 hour intercontinental flight – a technical development which was certainly unpredictable when our perceptual processing mechanisms evolved to what they are like today. Still, our visual system is prepared to adapt to changes and enables us to perceive and act efficiently no matter what the next visual impression will be.

8. Summary

The perception of faces is an essential aspect of our social life as it does not only enable us to recognise the faces of people who we already know but also allows for the perception of the gender, approximate age, emotional expression, and focus of attention of any familiar *and* unfamiliar face we meet. The accurate perception of this information is a fundamental basis of socially adequate behaviour and functioning human relations.

Despite the long tradition of research investigating both face recognition and the perception of face-related social information, the question of how we actually perceive such facial information is not yet completely resolved. A promising new approach of the past ~10 years is the investigation of face adaptation effects which allows for a better understanding of the processes underlying the perception of different information in faces.

The investigation of adaptation to certain stimulus attributes has a very long tradition in research on the processing of relatively basic physical stimulus attributes such as motion, orientation, or colour. The most prominent example of so-called aftereffects of adaptation is the waterfall illusion whose first mention is ascribed to Aristotle (*Parva Naturalia*): after prolonged exposition to downward motion we often perceive an illusory upward motion in a subsequently presented static visual image. The systematic investigation of aftereffects can reveal deep insight into the architecture of the visual system: the motion aftereffect has been shown to originate from selective adaptation to downward motion in downward-motion selective cell populations and from the resulting dominance of an unadapted opponent cell population selectively coding upward motion.

The systematic investigation of face adaptation effects in high-level vision has already been shown to be of similar value for our understanding of how distinct facial characteristics are perceived and mentally represented. For instance, paradigms investigating adaptation to identity in faces have found that faces are mentally represented in a multi-dimensional face space with a face-prototype at its centre (Leopold et al., 2001). Most importantly for the present work, studies on gaze adaptation revealed insight that eye gaze directed to the left and right seems to be processed by distinct cell populations (Jenkins et al., 2006; Seyama & Nagayama, 2006).

Research combining adaptation paradigms with modern electrophysiological and neuroimaging methods is only at its beginning but those studies that have already been conducted revealed promising new approaches to understanding the processing of complex face stimuli. Further, there are already a number of studies on fMRI adaptation, whereas the electrophysiological correlates of high-level adaptation have so far hardly been examined. Although a study investigating ERP correlates in a gender adaptation paradigm has already shown that the simultaneous application of both methods can be successfully combined (Kovács et al., 2006), the investigation of event-related correlates of other adaptation effects has so far been neglected. This approach, however, seems to be particularly promising since the combination of adaptation paradigms and electrophysiological recordings offers the possibilities to not only reveal functional subdivisions in the face perception system but also to determine their involvement in the different face processing stages with a superb time resolution.

The studies described in this thesis were designed to close this gap. Whereas Experiments 1 and 2 investigated the electrophysiological correlates of the eye gaze adaptation effect, Experiment 3 aimed at a further investigation of the nature of high-level adaptation effects in describing temporal aspects of gaze adaptation. Finally, Study 4 was conducted in order to further investigate the neural correlates of gender adaptation using a modified ERP adaptation paradigm which had been developed on the basis of the findings of Experiment 1 and was also applied in Experiment 2. A new experimental control condition aimed at disentangling the relative influences of general face adaptation and adaptation to specific facial characteristics (i.e. eye gaze direction and gender).

The series of experiments replicated and extended earlier findings on high-level face adaptation effects. Experiment 1 revealed a first insight into the neural correlates of gaze adaptation and suggested that direction-specific effects emerge not earlier than ~250 – 350 ms post stimulus onset. Further, the findings of that study suggested that the neural processing stages eliciting the N170 component are largely sensitive to face repetition as reflected in dramatically reduced N170 amplitudes in trials immediately following prior face presentation as compared to trials presented after longer intervals of a blank screen.

These observations motivated the application of a new control adaptation condition in Experiment 2 in which participants either adapted to direct gaze or to right gaze direction, therefore being presented with the same amount of face information in both conditions. The newly implemented direct gaze adaptation condition was found to lead to the same judgements of the direction of gaze in test faces as observed in a traditional pre-adaptation baseline, suggesting that the direct gaze adaptation condition served the purpose of a neutral control condition. The N170 amplitude in Experiment 2 was unaffected by general face adaptation effects which is in line with the hypothesis that the large N170 effects observed in Experiment 1 had been largely due to general face adaptation but not to gaze adaptation. The finding that only very small effects of gaze adaptation could be found in the N170 in Experiment 2 whereas correlates of gaze adaptation were more pronounced in the time interval of 250 – 350 ms can therefore be considered as further evidence that adaptation to gaze does not alter the processing of face stimuli before 250 ms. Greatest effects of gaze adaptation were observed in the late positive component ~400 to 600 ms after stimulus onset in which test stimuli gazing in the direction of adaptation were found to elicit smaller amplitudes than test stimuli gazing in unadapted directions. This pattern was interpreted to reflect a P3-like effect in terms of an easier context update or smaller information delivery of adapted stimuli leading to an emphasis of relatively new, i.e. unadapted, characteristics in faces which has been thought to reflect the neural basis of ‘novelty detection’ as a consequence of adaptation.

Experiment 3 investigated the time-course of gaze adaptation. Adaptation effects observed in response to test stimuli with small gaze deviations were characterised by a higher initial level and a more gradual decay than stimuli with larger gaze deviations. The decay of aftereffects in the perception of both small and larger gaze deviations was found to be best described by a negative exponential function further stressing the similarities in the characteristics of low-level and high-level adaptation processes.

Finally, Experiment 4 investigated the effects of adaptation to gender in voices and faces on the perception of facial gender. The study provided first evidence for a cross-modal adaptation effect as adaptation to male voices was found to bias the classification of gender of subsequently presented face stimuli. Again, only small correlates of gender adaptation could be observed in the N170 component, whereas a larger and more systematic pattern was found in the time range of the late positive component ~400 – 600 ms after stimulus onset. Here, test stimuli evoked more positive amplitudes when presented following male as compared to androgynous adaptation - an effect which was most pronounced for relatively female test stimuli. This finding supported the idea that the late effect might reflect an easier context update of test stimuli similar to the context provided by the adaptation stimuli. In line with the findings of Experiment 2, this effect seemed to be based on a categorical decision on ‘maleness’ versus ‘femaleness’ and did not differentiate between the smaller variations of gender in test stimuli.

To summarise, the findings confirmed the sensitivity of the N170 to general face information which is in line with assumptions that this processing stage mainly reflects the structural encoding of the face composition. The time interval of 250 – 350 ms after stimulus onset consistently revealed effects of gaze adaptation suggesting that this time window is crucial for the perception of gaze direction especially for the distinction between direct and averted gaze. This distinction is important because it has been found to play an important role also in interaction with emotion processing (Adams & Kleck, 2003; Adams & Kleck, 2005; but see Bindemann, Burton, & Langton, 2008) and general face judgements, for example concerning the attractiveness of faces (Conway et al., 2008; Jones et al., 2006). Finally, the late positive component in the time window of approximately 400 to 600 ms has consistently been found to be largely influenced by both eye gaze and gender adaptation. Here, test stimuli providing stimulus properties similar to the adaptor evoked significantly smaller amplitudes, a finding which might reflect the relatively easier context update and the relatively smaller informational value of test stimuli exhibiting the adapted property. This late effect is therefore proposed to be the neural correlate of ‘novelty detection’ which is assumed to be one of the major outcomes of adaptation.

9. Zusammenfassung

Die Wahrnehmung von Gesichtern ist ein wesentlicher Aspekt unseres sozialen Miteinander, denn sie ermöglicht uns nicht nur bekannte Personen zu erkennen, sondern gibt uns auch Aufschluss über das Geschlecht, das ungefähre Alter, den emotionalen Gesichtsausdruck und den Aufmerksamkeitsfokus jeder bekannten *und* unbekannten Person, die wir treffen. Die Wahrnehmung dieser Informationen ist einer der Grundsteine für sozial angemessenes Verhalten und somit auch für erfolgreiche zwischenmenschliche Beziehungen.

Obwohl die Forschung zur Erkennung von Gesichtern und zur Wahrnehmung der in ihnen enthaltenen sozial relevanten Informationen eine lange Tradition hat, ist noch immer nicht vollständig geklärt, wie diese Verarbeitung genau funktioniert. Ein viel versprechender Forschungsansatz der vergangenen etwa zehn Jahre ist die Untersuchung von so genannten Adaptationseffekten in der Wahrnehmung von Gesichtern, deren systematische Analyse ein genaueres Verständnis der Verarbeitung der verschiedenen in Gesichtern enthaltenen Informationen ermöglicht.

Die Untersuchung selektiver Adaptationseffekte hat eine lange Tradition in Forschungsarbeiten zur visuellen Verarbeitung relativ basaler physikalischer Stimuluseigenschaften, wie zum Beispiel Bewegung, Orientierung oder Farbe. Das wohl bekannteste Beispiel so genannter Adaptations-Nacheffekte ist die Wasserfalltäuschung, deren erste Erwähnung Aristoteles (Parva Naturalia) zugeschrieben wird: Nach längerer Präsentation von Abwärtsbewegung nehmen wir in einem statischen Bild eine illusorische Aufwärtsbewegung wahr.

Die systematische Untersuchung von Nacheffekten dieser Art kann ein größeres Verständnis der Organisation des visuellen Systems ermöglichen. So wurde zum Beispiel gezeigt, dass der Bewegungsnacheffekt aus der Adaptation von Zellpopulationen resultiert, welche selektiv auf abwärtsgerichtete Bewegungen reagieren. Ein Resultat dieser Adaptation ist die relative Dominanz von Aktivität in unadaptierten opponenten Zellverbänden, die Aufwärtsbewegungen verarbeiten. Dieses Ungleichgewicht zwischen adaptierten und unadaptierten opponenten Zellverbänden führt dann zu einer Wahrnehmungsillusion wie dem Bewegungsnacheffekt.

Es wurde gezeigt, dass die systematische Untersuchung von Gesichts-Adaptationseffekten ähnlich wertvoll sein kann für ein besseres Verständnis sowohl der Verarbeitungsmechanismen als auch der mentalen Repräsentation der verschiedenen in Gesichtern enthaltenen Informationen. So haben zum Beispiel Untersuchungen zur Adaptation an die Identität von Gesichtern gezeigt, dass diese in einem multidimensionalen Gesichter-Raum repräsentiert werden, in dessen Zentrum ein Gesichtsprototyp steht (Leopold et al., 2001). Von besonderer Bedeutung für die vorliegende Arbeit sind die Studien zur Blickrichtungsadaptation, die zeigten, dass Probanden selektiv an nach rechts bzw. nach links gerichteten Blick adaptieren (Jenkins et al., 2006; Seyama & Nagayama, 2006). Dies bedeutet, dass die Probanden nach vermehrter Konfrontation mit z.B. nach rechts abgewandter Blickrichtung für diese Richtung insensitiv wurden und Gesichter, die in die adaptierte Richtung blickten, als geradeaus schauend wahrnahmen. Diese Ergebnisse legten nahe, dass die verschiedenen Blickrichtungen von unterschiedlichen Zellpopulationen verarbeitet werden.

Die Erforschung von Adaptationsparadigmen in Kombination mit modernen elektrophysiologischen und bildgebenden Verfahren steckt noch in den Anfängen, doch die wenigen bereits durchgeführten Studien sind viel versprechend im Hinblick auf ihre Möglichkeiten das Verständnis der Verarbeitung von Gesichtern zu vergrößern. Insbesondere gibt es bereits eine Reihe von fMRI Studien zur Adaptation, während die elektrophysiologischen Korrelate von Adaptationsprozessen auf hohen Ebenen der visuellen Wahrnehmung bislang kaum untersucht wurden. Obwohl eine Studie zu den ERP-Korrelaten der Adaptation an das Geschlecht von Gesichtern bereits zeigte, dass beide Methoden erfolgreich kombiniert werden können (Kovács et al., 2006), wurde die Untersuchung der neuronalen Korrelate anderer Adaptationseffekte bislang vernachlässigt. Dieser Ansatz scheint jedoch besonders Erfolg versprechend, da die Kombination von Adaptationsparadigmen und elektrophysiologischen Aufzeichnungen nicht nur die Möglichkeit bietet selektiv adaptierende funktionale Einheiten innerhalb des Gesichterwahrnehmungssystems zu identifizieren, sondern auch deren Beitrag zu den verschiedenen Stufen der Wahrnehmung eines Gesichts mit einer exzellenten zeitlichen Auflösung zu bestimmen.

Die im Rahmen dieser Arbeit beschriebenen Studien haben begonnen diese Forschungslücke zu schließen. Während die Experimente 1 und 2 die elektrophysiologischen Korrelate der Blickrichtungsadaptation untersuchten, zielte Experiment 3 auf eine genauere Bestimmung der für diesen Adaptationseffekt geltenden zeitlichen Parameter. In Anlehnung an eine Studie von Kovács et al. (2006) diente Experiment 4 einer weiteren Untersuchung der neuronalen Korrelate der Adaptation an das Geschlecht eines Gesichts. Insbesondere untersuchte diese Studie die Modalitätsspezifität von Adaptationseffekten, indem sowohl Effekte der Adaptation an männliche Gesichter als auch an männliche Stimmen auf die anschließende Wahrnehmung des Geschlechts von Gesichtern erhoben wurden.

Die Serie von Studien konnte frühere Befunde zu Gesichtsadaptationseffekten replizieren und erweitern. Experiment 1 ermöglichte den bislang ersten Einblick in die neuronalen Korrelate von Blickrichtungsadaptation und legte nahe, dass richtungsspezifische Effekte der Adaptation in ereigniskorrelierten Potenzialen nicht vor ~250 – 350 ms auftreten. Des Weiteren zeigte die Studie, dass die neuronalen Generatoren der N170-Komponente in einem großen Ausmaß für die Wiederholung von Gesichtsinformation sensibel sind. Dies offenbarte sich in einer deutlich reduzierten Amplitude der N170 auf Teststimuli denen unmittelbar Adaptationsstimuli vorausgingen im Vergleich zu Teststimuli in der Kontrollbedingung, denen in Anlehnung an traditionelle Adaptationsparadigmen keine Adaptationsstimuli vorausgingen wodurch die Testgesichter in einem größeren zeitlichen Abstand präsentiert wurden.

Diese Befunde führten zur Anwendung einer neuen Kontrollbedingung in Experiment 2, in dem die Probanden entweder an Gesichter mit direktem Blick oder an Gesichter mit nach rechts gerichtetem Blick adaptierten und deshalb in beiden Versuchsbedingungen in demselben Ausmaß Gesichtsinformation wahrnahmen. Es zeigte sich, dass die neue Bedingung, in der Probanden auf direkte Blickrichtung adaptierten, zu denselben Einschätzungen der Blickrichtung von Teststimuli führte wie eine traditionelle Präadaptations-Kontrollbedingung, was ihre Eignung als neutrale Vergleichsbedingung unterstreicht. Durch die Einführung der alternativen Kontrollbedingung in Experiment 2 wurden dort die in Experiment 1 gefundenen großen Amplitudenunterschiede in der N170 nicht mehr beobachtet. Dies unterstützte die Hypothese, dass die Amplitudenunterschiede der N170 in Experiment 1 tatsächlich hauptsächlich Adaptationseffekte auf generelle Gesichtskonfiguration, nicht jedoch auf Blickrichtung darstellten. Zusammengenommen mit einem weiteren Ergebnis aus Experiment 2, nämlich den nur geringen Einflüssen von Blickrichtungsadaptation auf die Amplitude der N170 im Vergleich zum Zeitbereich von ungefähr 250 – 350 ms, legt dies nahe, dass Blickrichtungsadaptation die Verarbeitung von Gesichtern erst ab ca. 250 ms verändert. Sehr deutliche Korrelate der Blickrichtungsadaptation wurden erst in einer späten, positiven Komponente von ~400 – 600 ms gefunden, in der Teststimuli, deren Blick in die adaptierte Richtung gewandt war, deutlich geringere

Amplituden evozierten als Teststimuli, deren Blick in unadaptierte Richtungen gewandt war. Dieses späte Muster wurde im Sinne eines P3-Effekts interpretiert und könnte den relativ größeren Informationsgewinn durch vom Adaptationskontext abweichende Stimulusmerkmale reflektieren, was zu einer besonderen Betonung unadaptierter Stimuluscharakteristika führt und möglicherweise ein neuronales Korrelat der als Folge von Adaptation vorgeschlagenen *novelty detection* darstellt.

Experiment 3 untersuchte den Zeitverlauf von Blickrichtungsadaptation und konnte zeigen, dass Adaptationseffekte auf Teststimuli mit geringeren Abweichungen von direktem Blick (d.h. 5° Abweichung in die adaptierte Richtung) durch ein höheres Anfangsniveau und einen langsameren Verfall gekennzeichnet sind als solche auf Teststimuli mit größeren Abweichungen in der Blickrichtung (d.h. 10° Abweichung in die adaptierte Richtung). Für beide Abweichungen konnte der Verfall von Nacheffekten am besten mit einer negativen Exponentialfunktion beschrieben werden, wie sie auch für Nacheffekte bei basalen Stimuluscharakteristika berichtet wurde.

Experiment 4 untersuchte schließlich die Effekte von Adaptation an das Geschlecht von Stimmen und Gesichtern auf die Wahrnehmung anschließend präsentierter Gesichtsstimuli. Diese Studie konnte erste Evidenz für Adaptationseffekte zwischen Modalitäten liefern: sowohl die Adaptation an eine männliche Stimme als auch an ein männliches Gesicht erhöhten die Wahrscheinlichkeit, dass anschließend präsentierte Gesichter als weiblich klassifiziert wurden. Auch in dieser Studie wurden nur geringe Einflüsse von Adaptation auf die Amplitude der N170 gefunden, während deutlichere und sehr systematische Effekte von Adaptation in den ereigniskorrelierten Potenzialen erst im Zeitbereich von ~400 – 600 ms auftraten. Hier zeigte sich, dass Testgesichter, die nach Adaptation an männliche Gesichter präsentiert wurden, deutlich größere Amplituden evozierten als Testgesichter, die nach Adaptation an androgyne Gesichter gezeigt wurden. Dieser Effekt war am deutlichsten für relativ feminine Gesichter und unterstützte somit die Hypothese, dass der Adaptationseffekt in dieser späten Komponente den größeren Informationsgewinn durch vom Adaptationskontext stark unterschiedliche Gesichter darstellt. In Übereinstimmung mit den Befunden aus Experiment 2 schien der späte Adaptationseffekt auf einer kategorialen Einschätzung zwischen „Maskulinität“ und „Femininität“ zu beruhen und differenzierte nicht zwischen kleineren Variationen der Geschlechtsambiguität der Teststimuli.

Insgesamt unterstützten die Ergebnisse der hier berichteten Studien somit die Sensitivität der N170 Komponente für allgemeine Gesichtsinformationen unabhängig vom Geschlecht und der Blickrichtung der Gesichter. Dieses Ergebnis ist in Übereinstimmung mit Theorien, nach denen die Verarbeitungsstufe um ~170 ms in erster Linie die strukturelle Enkodierung von Gesichtern reflektiert. Das Zeitintervall um 250 – 350 ms wurde konsistent durch Blickrichtungsadaptation beeinflusst, ein Befund der impliziert, dass dieser Zeitbereich für die Wahrnehmung von Blickrichtungen von besonderer Relevanz ist. Insbesondere scheint in diesem Stadium eine Differenzierung zwischen direktem und abgewandtem Blick stattzufinden, die in verschiedenen früheren Studien, z.B. im Zusammenhang mit der Wahrnehmung von Emotionen, als besonders bedeutsam herausgestellt wurde (Adams & Kleck, 2003; Adams & Kleck, 2005). Schließlich wurden ebenfalls sehr konsistent Einflüsse von Adaptation in einem Zeitbereich um 400 – 600 ms gefunden. Hier konnte gezeigt werden, dass Teststimuli, deren Eigenschaften den jeweiligen Adaptationsstimuli sehr ähnlich waren, deutlich geringere Amplituden evozierten als Teststimuli, die den Adaptationsstimuli unähnlich waren. Dieses Ergebnis könnte eine einfachere Kontext-Aktualisierung bzw. einen geringeren Informationsgehalt von Stimuli mit einer adaptierten Merkmalsausprägung reflektieren. Aus diesem Grund scheint es plausibel, den späten Adaptationseffekt als neuronales Korrelat der *novelty detection* anzunehmen, welche als eines der wichtigsten Ergebnisse von Adaptation diskutiert wird.

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List of abbreviations

ANOVA	analysis of variance
BOLD	blood-oxygen level dependent
EEG	electroencephalography
ERP	event-related potential
EOG	electrooculogram
FDAE	face distortion aftereffect
FIAE	face identity aftereffect
FFA	fusiform face area
fMRI	functional magnetic resonance imaging
FRU	face recognition unit
HR-fMRI	high-resolution functional magnetic resonance imaging
ISI	interstimulus interval
MAE	motion aftereffect
MEG	magnetoencephalography
MPF	medial prefrontal cortex
PET	positron emission tomography
PIN	person identity node
PLW	point light walker
SD	standard deviation
SEM	standard-error of the mean
SR-fMRI	standard-resolution functional magnetic resonance imaging
STS	superior temporal sulcus
VCV	vowel-consonant-vowel
VPP	vertex positive potential

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Ehrenwörtliche Erklärung

Hiermit erkläre ich, dass mir die geltende Promotionsordnung der Fakultät für Sozial- und Verhaltenswissenschaften der Friedrich-Schiller-Universität Jena bekannt ist.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbst und ohne unzulässige Hilfe Dritter angefertigt habe. Alle von mir benutzten Hilfsmittel und Quellen sind in der Arbeit angegeben. Insbesondere habe ich hierfür nicht die Hilfe eines Promotionsberaters in Anspruch genommen und Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen von mir für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorliegenden Dissertation stehen.

Bei der Auswahl und Auswertung des Materials sowie bei der Herstellung des Manuskripts hat mich Prof. Dr. Stefan Schweinberger unentgeltlich unterstützt.

Die Arbeit wurde weder im In- noch im Ausland in gleicher oder ähnlicher Form für eine staatliche oder andere wissenschaftliche Prüfung eingereicht. Weder früher noch gegenwärtig habe ich an einer anderen Hochschule eine Dissertation eingereicht.

Ich versichere, dass ich nach bestem Wissen die reine Wahrheit gesagt und nichts verschwiegen habe.

Jena, den 17.11.2008